

HISTORICAL CHANGES IN THE OCCURRENCE AND DISTRIBUTION OF FRESHWATER MUSSELS IN KANSAS

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ABSTRACT—The surface waters of eastern and central Kansas once supported an impressive variety of native freshwater mussels, but a widespread decline in species richness accompanied the urban, industrial, and agricultural development of this region. Statewide mussel surveys implemented during the past two decades have shed new light on the scope and severity of this decline. Of the 48 mussel species originally known from Kansas, six are now extirpated, one lacks reproductively viable populations (i.e., faces imminent extirpation), and 38 others have suffered evident range reductions or a widespread thinning of former populations. Soil erosion and stream siltation, other forms of water and sediment pollution, physical habitat degradation, stream flow attenuation, and declines in the native fishes serving as biological hosts for larval mussels all have contributed to these changes. Dams and other impediments to fish migration now hinder the reestablishment of mussel colonies following prolonged droughts and major water pollution events. Some mussel populations in this region display unique morphological, developmental, and genetic attributes, implying their continued attrition may lead to the eventual loss of distinctive forms or subspecies.

Key Words: aquatic habitat restoration, freshwater mussels, prairie streams, zoogeographical surveys

INTRODUCTION

Freshwater mussels (Mollusca: Bivalvia: Unionoida) inhabit many of the world's inland waters but attain their greatest taxonomic diversity in the perennial streams of eastern North America (Bogan 1993). A few dozen species range westward into the Great Plains, where they achieve significant population densities and perform several crucial ecological functions. For example, mussels in this region provide an important source of food for

numerous predatory fish and wildlife species, and their spent shells afford shelter and egg attachment sites for a wide assortment of aquatic and semiaquatic organisms (Murray and Leonard 1962; Cvancara 1983; Howells et al. 1996). As filter feeders subsisting primarily on suspended bacteria, algae, and organic detritus, mussels enhance the clarity of the water column and facilitate the transfer of nutrients from the water to the bottom substrate and its affiliated biological community (Strayer et al. 1994; Vaughn et al. 2004; Vaughn and Spooner 2006). As active

burrowers, mussels also play a role in the homogenization and aeration of the surficial sediment layer (McCall and Tevesz 1979; McCall et al. 1995). Mussels often form dense beds in favorable aquatic habitats. These features may contain thousands of buried or partially buried individuals, collectively dominating the local benthic biomass and effectively stabilizing the bottom substrate during periods of high stream flow (Strayer et al. 1994; Smith 2001; Zimmerman and de Szalay 2007).

Most freshwater mussel species undergo an extraordinary life cycle that involves a parasitic larval life stage and an elaborate mechanism for transferring larvae to a suitable vertebrate host, usually a fish (Smith 2001; Obermeyer et al. 2006). Gravid females in some species possess anatomical modifications that resemble small fish or other edible organisms, and these act as lures to attract prospective host fish (e.g., Kraemer 1970). In many other instances, larval mussels (glochidia) are embedded within gelatinous masses (conglutinates) mimicking worms or other animals preyed upon by the host species (e.g., Barnhart 1997). Any fish contacting a gravid mussel or ingesting a conglutinate released into the water runs the risk of being infested with hundreds of glochidia. If an infested fish is a compatible host, the glochidia rapidly encyst within its gill or fin membranes, then transform over a period of weeks or months into fully formed juvenile mussels. These eventually detach from the host, settle to the bottom substrate, and begin their lives as free-living organisms. Mussels typically mature within a few years, and maximum life spans may range from less than a decade to more than a century, depending on the species (Smith 2001; Obermeyer et al. 2006). Because these animals spend their entire juvenile and adult lives in the same general location, their populations are unusually sensitive to local changes in water and sediment quality, physical habitat condition, and fish community composition. Accordingly, freshwater mussel communities provide insight into the prevailing environmental condition and often garner the attention of aquatic ecologists and natural resource managers.

More than 40 mussel species reach or approach their western distributional limits in Kansas (Murray and Leonard 1962). Some species range widely across the state and maintain large and conspicuous populations in numerous water bodies. Others are exceedingly rare and known only from a few locations. The first mussel surveys in Kansas were implemented shortly after the settlement of the state (Call 1885a, 1885b, 1885c, 1886, 1887; Popenoe 1885). Subsequent statewide surveys, and more intensive biological studies focusing on specific

watersheds and stream reaches, added significantly to the known ranges of many taxa (e.g., Scammon 1906; Clark and Gillette 1911; Isely 1925; Grinnell 1942; Franzen and Leonard 1943; Leonard 1943; Murray and Leonard 1962; Branson 1966; Miller and Hibbard 1972; Liechti and Huggins 1977; Cope 1979, 1981; Schuster 1979; Schuster and DuBois 1979; Hacker 1980; Metcalf 1980; Claassen 1981; Distler and Bleam 1995; Obermeyer et al. 1997; Hoke 1997, 2005; Bleam et al. 1998; Bergman et al. 2000; VanLeeuwen and Arruda 2001). During the latter half of the 20th century, a number of archeological and paleontological (Pleistocene-oriented) studies provided additional data on the historical and prehistorical distributions of mussels in this region (e.g., Kivett 1953; Wedel 1959; Hibbard and Taylor 1960; Miller 1966, 1970; Wilmeth 1970; Bradley 1973; Warren 1974; Thies 1981; Witty 1983; Dorsey 2000).

Recent investigations have documented an alarming decline in the mussel fauna of several major watersheds in Kansas (e.g., Hunter 1993; Distler and Bleam 1995; Hoke 1996, 1997, 2004, 2005; Obermeyer et al. 1997; Bergman et al. 2000; Reed 2002; Mosher 2006; Tiemann 2006; Wolf and Stark 2008). Concerns related to the long-term survival of mussels have led to the designation of 23 species as threatened or endangered (T/E) or as species in need of conservation within the state (KDWP 2005). Thus far, mussel conservation efforts have focused on the development, review, and initial implementation of recovery plans for eight T/E species (Obermeyer 2000, 2002). These plans call for the physical restoration of key aquatic habitats, emphasize the need for major improvements in surface water and sediment quality, and propose artificial propagation and restocking programs for selected T/E taxa. Laboratory propagation methods already have been developed for several mussel species (e.g., O'Beirn et al. 1998; Barnhart 2006), and pilot restocking projects have led to the successful augmentation of mussel populations in a few restricted stream reaches (e.g., Barnhart 2002).

Upcoming recovery efforts will endeavor to restore, to the fullest practicable extent, the diverse mussel communities once found in this region (Simmons 2008). Attainment of this goal will require an accurate understanding of the current and former distributions of each native mussel species. To foster such an understanding, we report on the results of an extensive series of mussel surveys implemented over an 18-year period, examine key records from earlier surveys, and present a set of detailed maps illustrating the contemporary and historical ranges of the state's known indigenous mussels and two introduced (but widely established) bivalves. We conclude our report

by reviewing the major factors now limiting the survival and distribution of freshwater mussels in Kansas.

METHODS

Statewide mussel surveys were performed by the Kansas Department of Health and Environment (KDHE) and the Kansas Department of Wildlife and Parks (KDWP) during the years 1990–2007 and 1995–2007, respectively. KDHE employed a targeted sampling design that focused initially on larger, perennial streams and later included many intermittent streams and publicly owned lakes and wetlands (KDHE 2005b, 2005c, 2007a). By December 2007, 800 sites (740 stream reaches, 60 lakes and wetlands) had been surveyed for mussels using this targeted sampling approach. To enhance the documentation of rarer taxa, surveys were repeated at least twice in 128 stream reaches, most supporting comparatively diverse mussel communities. Ninety-eight randomly selected stream reaches also were surveyed during 2006 and 2007 as part of a newly implemented probabilistic monitoring program (KDHE 2007b). Surveys performed by KDWP relied primarily on a probabilistic sampling design emphasizing smaller, wadeable streams (e.g., Obermeyer 1997). By the end of 2007, KDWP had completed surveys in 1,294 stream reaches. Eighteen additional stream reaches were sampled in conjunction with annual workshops hosted by this agency (e.g., Miller 2004). Altogether, 2,210 sites were surveyed by the two agencies.

All KDHE and KDWP surveys were implemented by two or more aquatic biologists familiar with the regional mussel fauna, and all were conducted during periods of limited precipitation and runoff when most aquatic habitats were amenable to visual or tactile examination. Stream surveys were concluded following the examination of all targeted mussel habitats (primarily riffles, runs, shoals, chutes, side channels, and backwaters). Sampling reaches generally ranged in length from 100 m to 500 m (KDHE) or from 100 m to 300 m (KDWP), depending on stream size, habitat complexity, and access considerations. Surveys conducted in lakes and wetlands were restricted to shallow (≤ 1.0 m) littoral areas, and most were performed in the general vicinity of boat ramps or other readily accessible locations. At essentially all survey sites, live mussels were sought by wading and visually examining the bottom substrate in shallower reaches, by manually sweeping and probing the surficial substrate in deeper or more turbid locations, and by manually excavating and sifting small volumes of substrate in selected promising habitats (e.g., gravelly riffles). Live mussels encountered

during the surveys were identified and released onsite. Remnant shell materials (vacant shells and disarticulated valves left by dead mussels) were collected from lake and wetland margins, stream shorelines, and sand and gravel bars. Representative shell collections were retained by KDHE and archived at the agency's headquarters in Topeka, KS (KDHE 2007a). KDWP deposited selected vouchers at the Sternburg Museum of Natural History in Hays, KS, and the University of Kansas Natural History Museum and Biodiversity Research Center in Lawrence, KS.

Mussel databases were developed and maintained independently by KDHE and KDWP but merged for the purposes of this study. Site-specific data on the presence or absence of live mussels and on the condition of any recovered shell materials were used to evaluate the distributional status of each native mussel species. The documentation of live individuals, unweathered shells, or both at a given sampling site was interpreted as evidence of an extant mussel population. The presence of only weathered shell materials (typically, disarticulated valves with eroded margins, flaking periostracum, faded nacre, and worn pseudocardinal and lateral teeth) or subfossil shell materials (typically, heavily worn, partially delaminated, chalky valves) was interpreted as evidence of an extirpated population (KDHE 2007a). At sites sampled on three or more occasions ($N = 93$), changes in mussel diversity over time were evaluated by comparing the number of species represented by live individuals or unweathered shells to the total number of documented mussel species, that is, by comparing observed taxa richness (OR) to expected taxa richness (ER). Calculation of the ratio OR/ER allowed sites to be ranked according to their degree of departure from the expected richness condition. Maps (1:5.5 million scale) illustrating the current and former ranges of individual mussel species were created using ArcGIS software (version 9.3). Stream coverages represented in these maps were adapted from the U.S. Geological Survey National Hydrography Dataset (U.S. Geological Society 2007). Outlines of the 12 major river basins in Kansas (KWO 1985) were based on aggregated hydrological unit code (level 8) watershed boundaries (Seaber et al. 1987).

An extensive literature review was performed as part of this study (*see* References). This effort focused primarily on earlier mussel surveys conducted in Kansas and secondarily on surveys covering the adjacent portions of neighboring states (e.g., Aughey 1877; Simpson 1900, 1914; Utterback 1915, 1916; Isely 1925; Branson 1982, 1983, 1984; Hoke 1983, 2000; Oesch 1984; Wu

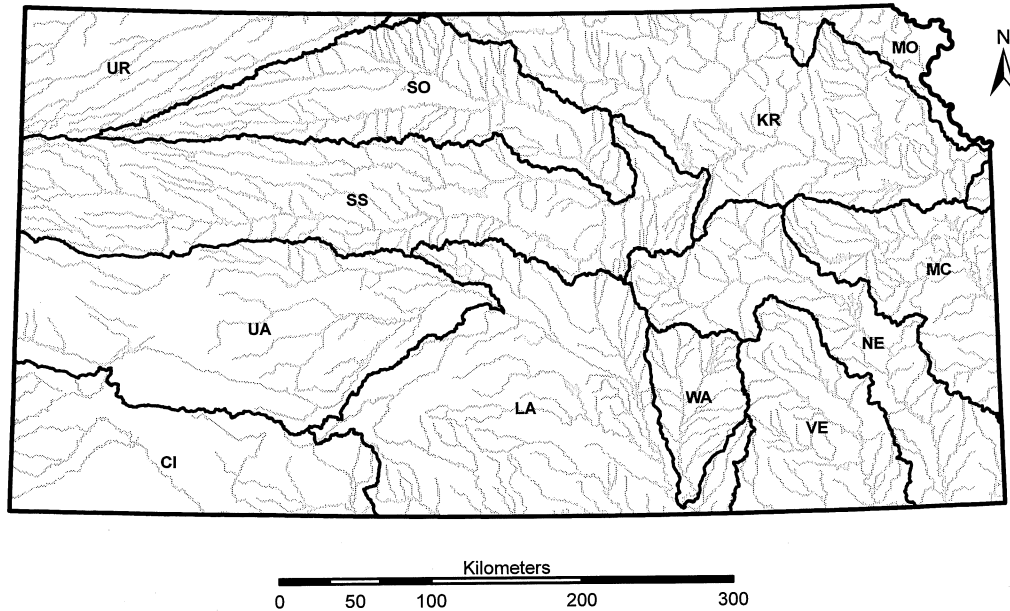


Figure 1. Major river basins in Kansas: Cimarron (CI), Kansas/Lower Republican (KR), Lower Arkansas (LA), Marais des Cygnes (MC), Missouri (MO), Neosho (NE), Smoky Hill/Saline (SS), Solomon (SO), Upper Arkansas (UA), Upper Republican (UR), Verdigris (VE), and Walnut (WA).

1989; Cordeiro 1999; Cordeiro et al. 2007). Selected in-state records were added to the geographical database to augment the distributional maps developed using the KDHE/KDWP survey data. Records from archeological and paleontological studies also were included if, in the express opinion of the reporting scientists, the recovered shell materials were derived originally from water bodies near the study sites (e.g., Wedel 1959; Miller 1970; Thies 1981; Dorsey 2000; Warren and Holen 2007). Mussel species documented immediately outside the state, but not within the state, were designated as “possibly native” to Kansas. However, these unconfirmed species were not represented in the final distributional maps.

Several natural history museums and universities were visited or contacted to verify unusual records encountered during the literature review. These institutions included the Field Museum of Natural History (FMNH), Florida Museum of Natural History (FLMNH), Illinois Natural History Survey (INHS), Kansas Biological Survey (KBS), National Museum of Natural History (NMNH), Notebaert Nature Museum (NNM), Ohio State University Museum of Biological Diversity (OSUM), Sternburg Museum of Natural History (SMNH), University of Kansas Natural History Museum and Biodiversity Research Center (KUNHM), University of Michigan Museum of Zoology (UMMZ), University of Nebraska State Museum (UNSM), and Wichita State University

Department of Biological Sciences (WSU). Four institutions (FLMNH, OSUM, NMNH, and UMMZ) loaned key vouchers to KDHE for extended examination. Most museum and university specimens were accompanied by labels indicating collection dates and localities, and this information was added selectively to the geographical database. During database entry, obsolete taxonomic synonyms encountered during the literature review and institutional searches were converted to the currently accepted scientific nomenclature (Turgeon et al. 1998; Eberle 2007a).

RESULTS

Altogether, 16,836 mussel occurrence records were generated during the KDHE/KDWP surveys. Live mussels, unweathered shells, or both were documented in each of the state’s 12 major river basins (Fig. 1) and at 1,165 survey sites (53% of all sites). Another 220 sites (10%) produced only weathered or subfossil shell materials, and the remaining 825 sites (37%) yielded no evidence of mussels (Fig. 2). Forty-two mussel species were represented by live individuals and recent shells, whereas one species (*Obovaria olivaria*) was represented solely by weathered and subfossil shell materials (Table 1). Of the 93 stream reaches sampled on three or more occasions, only 13 seemingly supported their

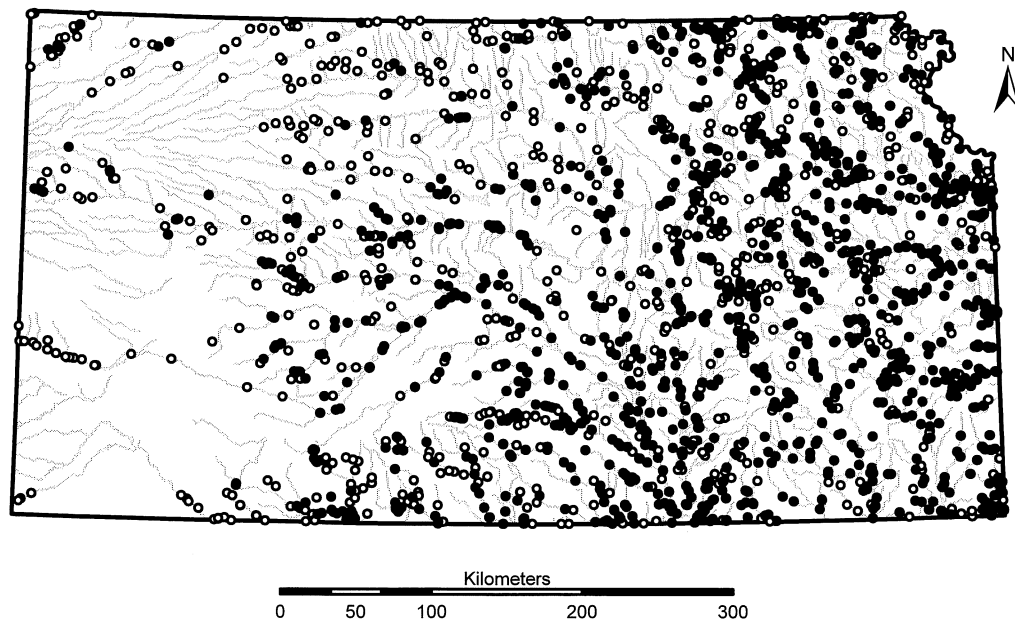


Figure 2. Sites sampled for freshwater mussels by the Kansas Department of Health and Environment and the Kansas Department of Wildlife and Parks (1990–2007). Solid circles represent sites that produced live individuals, remnant shell materials, or both. Open circles represent sites that yielded no evidence of mussels.

entire historical complement of mussel species (i.e., OR/ER = 1.0). Taxa richness evidently had declined by at least 25% in 40 stream reaches and by at least 50% in seven stream reaches. Table 2 presents basin affiliations, geographical coordinates, and OR/ER ratios for selected sampling locations, including all stream reaches specifically mentioned in this report.

Streams in the southeastern portion of the state generally exhibited the highest mussel diversity (Appendix 1, Figs. A1–A43). Individual sampling sites on Pottawatomie Creek, Cedar Creek (Chase County), and the Caney, Cottonwood, Fall, Little Osage, Marais des Cygnes, Marmaton, Neosho, Spring, and Verdigris rivers each produced evidence of 20 to 29 former species and 11 to 26 current species. Surveys conducted in northeastern Kansas likewise indicated a formerly diverse, but more heavily impacted, mussel fauna. For example, sites on West Branch Mill Creek, Vermillion Creek, and the Big Blue, North Fork Black Vermillion, (lower) Smoky Hill, South Fork Big Nemaha, Wakarusa, and Wolf rivers each produced evidence of 15 to 18 former species and 4 to 16 current species. Sites in central and western Kansas supported less diverse mussel assemblages, ranging upward to 11 former species and nine recent species (Little Arkansas River near Valley Center, KS). We regarded our historical richness estimates for sites in this region as conservative, given that some previous surveys and

archeological studies had indicated a more diverse pre-settlement fauna (e.g., Distler and Bleam 1995; Dorsey 2000).

Museum vouchers (and one privately owned voucher) examined during our study confirmed the historical presence of the following additional mussel species: *Alasmidonta viridis*, *Cumberlandia monodonta*, *Epioblasma triquetra*, *Lasmigona compressa*, and *Quadrula fragosa* (Table 1; Fig. A44). A single, well-preserved specimen of *Lampsilis higginsii* (I. Lea, 1857) also was encountered during the institutional searches (FLMNH 269580), but the reported collection location (“Wichita”) was well outside this mussel’s previously reported range and considered suspect (cf. Cummings and Mayer 1992). Vouchers were not located for several species reported in the historical literature, but known populations in neighboring states and/or detailed shell descriptions accompanying some of the original reports suggested that *Fusconaia ebena* (I. Lea, 1831), *Lampsilis abrupta* (Say, 1831), *Lampsilis satura* (I. Lea, 1852), *Leptodea leptodon* (Rafinesque, 1820), and *Plethobasus cyphus* (Rafinesque, 1820) may have occurred formerly in Kansas (Call 1885b, 1885c, 1886; Scammon 1906; Simpson 1914; Hoke 1983; Oesch 1984; Cummings and Mayer 1992). In-state records for *Lampsilis reeveiana brevicula* (Call, 1887) and *Toxolasma lividus* (Rafinesque, 1831) were not encountered during the literature review, and

TABLE 1
FRESHWATER MUSSELS INDIGENOUS TO KANSAS

Family/subfamily/scientific name	Common name	Status	Figure	Remarks (including key vouchers)
Margaritiferidae				
Cumberlandinae				
<i>Cumberlandia monodonta</i> (Say, 1829)*	Spectaclecase	Extirpated	A44	• KUNHM 001247 (Mulhern et al. 2002)
Unionidae				
Ambleminae				
<i>Amblema plicata</i> (Say, 1817)	Threeridge	Declining	A3	• Heavily harvested in Kansas, but moratorium on harvest enacted in 2003 (Mosher 2007; Miller and Mosher 2008)
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)	Purple wartyback	Stable	A7	• Rare and confined to one stream reach in Kansas
<i>Elliptio dilatata</i> (Rafinesque, 1820)	Spike	SINC	A10	
<i>Fusconaia flava</i> (Rafinesque, 1820)	Wabash pigtoe	SINC	A11	• Some (perhaps all) Kansas populations genetically distinct (Burdick and White 2007)
<i>Fusconaia ozarkensis</i> (Call, 1887)	Ozark pigtoe	Stable	A12	• Rare and confined to one stream reach in Kansas
<i>Megaloniais nervosa</i> (Rafinesque, 1820)	Washboard	SINC	A22	
<i>Pleurobema sintoxia</i> (Rafinesque, 1820)	Round pigtoe	SINC	A25	
<i>Quadrula cylindrica cylindrica</i> (Say, 1817)	Rabbitsfoot	E	A31	
<i>Quadrula fragosa</i> (Conrad, 1835)*	Winged mapleleaf	Extirpated	A44	• UMMZ 75811 (see also Bleam et al. 1998; Hoke 2004, 2005)
<i>Quadrula metanevra</i> (Rafinesque, 1820)	Monkeyface	Declining	A32	• Remains abundant in a few stream reaches; remarks for <i>A. plicata</i> , above, also apply to this species
<i>Quadrula nodulata</i> (Rafinesque, 1820)	Wartyback	SINC	A33	
<i>Quadrula pustulosa pustulosa</i> (I. Lea, 1831)	Pimpleback	Declining	A34	• Taxonomy of <i>Q. pustulosa</i> remains unresolved; some populations in Kansas may be genetically distinct
<i>Quadrula quadrula</i> (Rafinesque, 1820)	Mapleleaf	Declining	A35	• Still widespread, but <i>Q. quadrula</i> form <i>nobilis</i> considered extirpated in Kansas (Couch 1997); remarks for <i>A. plicata</i> , above, also apply to this species
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	Pistolgrip	Declining	A38	
<i>Unio merus tetralasmus</i> (Say, 1831)	Pondhorn	Declining	A41	• Still widespread; locally abundant in ponds, small lakes, and intermittent streams with permanent pools
Anodontinae				
<i>Alasmodonta marginata</i> Say, 1818	Elktoe	E	A2	
<i>Alasmodonta viridis</i> (Rafinesque, 1820)*	Slippershell	Extirpated	A44	• OSUM 66155 (Bleam and Distler 1996)
<i>Anodonta suborbiculata</i> Say, 1831	Flat floater	E	A4	• Sporadically abundant in a few oxbows, marshes, and floodplain ponds
<i>Anodontoides ferussacianus</i> (I. Lea, 1834)	Cylindrical papershell	SINC	A5	• Seemingly on verge of extirpation in Kansas
<i>Arcidens confragosus</i> (Say, 1829)	Rock pocketbook	T	A6	
<i>Lasmigona complanata complanata</i> (Barnes, 1823)	White heelsplitter	Declining	A17	• Still widespread; common in some small streams
<i>Lasmigona compressa</i> (I. Lea, 1829)*	Creek heelsplitter	Extirpated	A44	• A single, unnumbered voucher retained by Hoke (1996)
<i>Lasmigona costata</i> (Rafinesque, 1820)	Flutedshell	T	A18	
<i>Pyganodon grandis</i> (Say, 1829)	Giant floater	Declining	A30	• Still widespread; locally abundant in ponds, small lakes, and intermittent streams with permanent pools
<i>Strophitus undulatus</i> (Say, 1817)	Creeper	SINC	A36	
<i>Utterbackia imbecillis</i> (Say, 1829)	Paper pondshell	Declining	A42	• Still widespread; locally abundant in ponds and small lakes
Lampsilinae				
<i>Actinonaias ligamentina</i> (Lamarck, 1819)	Mucket	E	A1	
<i>Cyprogenia aberti</i> (Conrad, 1850)	Western fanshell	E	A8	• Kansas populations genetically distinct (Eckert 2003; Serb 2006)
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	Butterfly	T	A9	
<i>Epioblasma triquetra</i> (Rafinesque, 1820)*	Snuffbox	Extirpated	A44	• NMNH 743156 (Scammon 1906)
<i>Lampsilis cardium</i> Rafinesque, 1820	Plain pocketbook	Declining	A13	
<i>Lampsilis rafinesqueana</i> Frierson, 1927	Neosho mucket	E	A14	• Kansas may support largest remaining population (Angelo et al. 2007)
<i>Lampsilis siliquoidea</i> (Barnes, 1823)	Fatmucket	SINC	A15	• Historically ranked among the state's most abundant mussels (Call 1887; Scammon 1906)
<i>Lampsilis teres</i> (Rafinesque, 1820)	Yellow sandshell	SINC	A16	
<i>Leptodea fragilis</i> (Rafinesque, 1820)	Fragile papershell	Declining	A19	• Still widespread; locally abundant in streams
<i>Ligumia recta</i> (Lamarck, 1819)	Black sandshell	Nearly extirpated	A20	• One live individual reported from Kansas in 2002, the first since 1956 (Angelo and Cringan 2003)
<i>Ligumia subrostrata</i> (Say, 1831)	Pondmussel	Declining	A21	• Locally abundant in ponds, small lakes, and small streams
<i>Obliquaria reflexa</i> Rafinesque, 1820	Threehorn wartyback	Declining	A23	• Locally common in a few large streams
<i>Obovaria olivaria</i> (Rafinesque, 1820)	Hickorynut	Extirpated	A24	• Last live individuals in Kansas observed around 1900 (Scammon 1906)
<i>Potamilus alatus</i> (Say, 1817)	Pink heelsplitter	Declining	A26	• Locally common in streams
<i>Potamilus ohioensis</i> (Rafinesque, 1820)	Pink papershell	Stable	A27	• Locally common in streams and a few large reservoirs
<i>Potamilus purpuratus</i> (Lamarck, 1819)	Bleufer	Declining	A28	• Locally common in streams; remarks for <i>A. plicata</i> , above, also apply to this species
<i>Ptychobranchius occidentalis</i> (Conrad, 1836)	Ouachita kidneyshell	T	A29	
<i>Toxolasma parvus</i> (Barnes, 1823)	Lilliput	Declining	A37	• Locally common in ponds, lakes, and small streams
<i>Truncilla donaciformis</i> (I. Lea, 1828)	Fawnsfoot	SINC	A39	
<i>Truncilla truncata</i> Rafinesque, 1820	Deertoe	SINC	A40	
<i>Venustaconcha ellipsiformis</i> (Conrad, 1836)	Ellipse	E	A43	• Kansas populations genetically distinct (Barnhart 2001)

Notes: Most listed species were encountered as live individuals, remnant shell materials, or both during field surveys performed by KDHE and KDWP (1990–2007). The remaining species, denoted by asterisks (*), were confirmed on the basis of museum (or privately owned) vouchers examined during this study. Although not specifically noted above, taxa listed as endangered (E), threatened (T), or species in need of conservation (SINC) have exhibited declining distributions in Kansas (Appendix 1).

TABLE 2
HISTORICAL DECLINES IN MUSSEL SPECIES RICHNESS
(SELECTED STREAM REACHES, KANSAS)

Basin	Stream reach	County	Latitude	Longitude	N	OR	ER	OR/ER
CI	Cimarron River near Forgan (OK)	Meade	37.01163	-100.49189	4	0	0	—
KR	Big Blue River near Oketo	Marshall	39.95781	-96.60998	18	11	16	0.69
	N. Fork Black Vermillion River near Frankfort	Marshall	39.64975	-96.48149	41	11	17	0.65
	Vermillion Creek near Louisville	Pottawatomie	39.25619	-96.24972	10	8	15	0.53
	Wakarusa River near Richland	Shawnee	38.89181	-95.59458	25	16	18	0.89
	West Branch Mill Creek near Alma	Wabaunsee	39.00142	-96.28354	28	10	15	0.67
LA	Arkansas River near Haven	Reno	37.94641	-97.77510	18	3	4	0.75
	Cowskin Creek near Wichita	Sedgwick	37.64260	-97.44624	17	10	10	1.00
	Little Arkansas River near Valley Center	Sedgwick	37.83215	-97.38802	16	9	11	0.82
MC	Little Osage River near Fulton	Bourbon	38.00091	-94.68572	6	18	21	0.86
	Marais des Cygnes River near Ottawa	Franklin	38.61132	-95.20639	14	16	24	0.67
	Marmaton River near Fort Scott	Bourbon	37.85588	-94.63097	14	14	21	0.67
	Pottawatomie Creek near Lane	Franklin	38.44058	-95.07472	21	26	27	0.96
MO	Blue River near Stanley	Johnson	38.84233	-94.61247	19	12	15	0.80
	S. Fork Big Nemaha River near Bern	Nemaha	39.95873	-96.03522	10	9	17	0.53
	Wolf River near Sparks	Doniphan	39.84930	-95.18084	8	8	15	0.53
NE	Cedar Creek near Cedar Point	Chase	38.22370	-96.83128	23	18	21	0.86
	Cottonwood River near Emporia	Lyon	38.36545	-96.09208	17	13	25	0.52
	Neosho River near Chetopa	Labette	37.03693	-95.08108	18	23	29	0.79
	Spring River near Crestline	Cherokee	37.17868	-94.64152	25	25	26	0.96
SO	N. Fork Solomon River near Portis	Osborne	39.55428	-98.69211	17	5	5	1.00
	Solomon River near Niles	Ottawa	38.96909	-97.47637	22	6	7	0.86
	S. Fork Solomon River near Osborne	Osborne	39.42758	-98.65746	24	4	4	1.00
SS	Saline River near New Cambria	Saline	38.87471	-97.53859	23	5	8	0.63
	Smoky Hill River near Grandview Plaza	Geary	39.02827	-96.80449	17	4	16	0.25
UA	Arkansas River near Kinsley	Edwards	37.92791	-99.37544	3	1	1	1.00
UR	S. Fork Republican River near St. Francis	Cheyenne	39.67186	-102.01326	3	0	0	—
VE	Caney River near Elgin	Chautauqua	37.00375	-96.31618	7	16	20	0.80
	Fall River near Neodesha	Wilson	37.39700	-95.67900	15	24	28	0.86
	Otter Creek near Climax	Greenwood	37.70846	-96.22415	5	12	19	0.63
	Verdigris River near Sycamore	Montgomery	37.32676	-95.68463	17	24	28	0.86
WA	Rock Creek near Rock	Cowley	37.42603	-97.00569	5	6	9	0.67
	Walnut River near Gordon	Butler	37.58886	-97.00027	17	13	16	0.81

Notes: "N" refers to the number of onsite mussel surveys performed by KDHE during 1990–2007, "OR" to the number of mussel species represented by live individuals, unweathered shell materials, or both, and "ER" to the total number of documented mussel species (see text). River basin abbreviations are defined in Figure 1.

these two species evidently lacked museum vouchers from the state. However, both have been reported from the Spring River (Neosho) Basin in southwestern Missouri less than 35 km upstream of Kansas (Oesch 1984; Obermeyer et al. 1997; Angelo et al. 2007).

Formerly, some *Quadrula pustulosa* specimens from Kansas were assigned to the subspecies *Q. pustulosa*

mortoni (Conrad, 1835) (OSUM 33086 and 48398). A southern congener, *Quadrula houstonensis* (I. Lea, 1859), also was reported from the state by Call (1885b). Although several *Quadrula* specimens encountered during the KDHE and KDWP surveys resembled *Q. pustulosa mortoni* or *Q. houstonensis*, we opted to assign all such specimens to *Q. pustulosa pustulosa* pending further

investigation (Fig. A34). Historical accounts of *Actinonaias ligamentina* in the Neosho and Verdigris basins were attributed in our study to the superficially similar species, *Lampsilis rafinesqueana*. The occurrence of *L. rafinesqueana* in Kansas was recognized originally during the 1970s (e.g., Cope 1979). Most specimens collected before that time were assigned mistakenly to *A. ligamentina* or one of its earlier synonyms (UMMZ 46137, 52426, 107752, 168722, 231665; Call 1886; Scammon 1906; Grinnell 1942; Murray and Leonard 1962; cf. Eberle 2007a). *Lampsilis rafinesqueana* and *A. ligamentina* currently maintain non-overlapping distributions within the state (Figs. A1 and A14).

Previous reports of *Potamilus alatus* in the Neosho and Verdigris basins (e.g., Murray and Leonard 1962; Liechti and Huggins 1977) and *Potamilus purpuratus* in the Kansas/Lower Republican and Marais des Cygnes basins (e.g., Popenoe 1885; Liechti and Huggins 1977; Hoke 2005) were not substantiated during our study. Because the conchological attributes of *P. alatus* and *P. purpuratus* are variable, and in some individuals nearly indistinguishable, we questioned earlier records for these species from the above-mentioned basins. In preparing the distributional maps for this report, we elected to assign all historical records for *P. alatus* in the Neosho and Verdigris basins to *P. purpuratus* (Fig. A28). Conversely, historical records for *P. purpuratus* in the Kansas/Lower Republican and Marais des Cygnes basins were assigned to *P. alatus* (Fig. A26). More definitive (e.g., mitochondrial DNA-based) studies of these two species would be useful for clarifying their current ranges in Kansas (see Burdick and White 2007).

Most mussel species in the state have undergone an evident decline in geographical distribution. *Actinonaias ligamentina*, *Alasmidonta marginata*, *Anodontoides ferussacianus*, *Arcidens confragosus*, *Cyprogenia aberti*, *Lasmigona costata*, *Quadrula cylindrica cylindrica*, and *Venustaconcha ellipsiformis* each are relegated to one or two population centers but occupied a larger range in the past (Appendix 1). Only a single live *Ligumia recta* was encountered during our study, implying that this formerly widespread species now lacks reproductively viable populations in Kansas (Fig. A20) (Angelo and Cringan 2003). Other species exhibiting marked range contractions or a general thinning of former populations were *Amblesma plicata*, *Fusconaia flava*, *Lampsilis cardium*, *Lampsilis rafinesqueana*, *Lampsilis siliquoidea*, *Lampsilis teres*, *Ligumia subrostrata*, *Pleurobema sintoxia*, *Ptychobranhus occidentalis*, *Strophitus undulatus*, *Toxolasma parvus*, *Truncilla truncata*, and *Uniomerus*

tetralasmus (Appendix 1). In certain watersheds where they were once common, some of these species have been eliminated outright (e.g., *L. cardium* in the Kansas/Lower Republican Basin, Fig. A13; *S. undulatus* in the Walnut Basin, Fig. A36), or they now occur as sparsely scattered individuals (e.g., *L. siliquoidea* in the Kansas/Lower Republican Basin, Fig. A15; *T. truncata* in the upper Neosho Basin, Fig. A40).

Seventeen additional mussel species (*Anodonta suborbiculata*, *Ellipsaria lineolata*, *Elliptio dilatata*, *Lasmigona complanata complanata*, *Leptodea fragilis*, *Megalonaias nervosa*, *Obliquaria reflexa*, *P. alatus*, *P. purpuratus*, *Pyganodon grandis*, *Quadrula metanevra*, *Quadrula nodulata*, *Q. pustulosa pustulosa*, *Quadrula quadrula*, *Tritogonia verrucosa*, *Truncilla donaciformis*, and *Utterbackia imbecillis*) have experienced less dramatic declines, generally involving the loss of isolated headwater or peripheral populations (Appendix 1). Only three species appear to have maintained their presettlement distributions in Kansas: *Cyclonaias tuberculata* and *Fusconaia ozarkensis* still occur in restricted stream reaches along the Kansas-Missouri border (Figs. A7 and A12), whereas *Potamilus ohioensis* continues to range throughout much of the state (Fig. A27). Some authors have suggested that *P. ohioensis* is expanding its distribution in northwestern Kansas (e.g., Bergman et al. 2000). However, shells recovered from archeological sites in the Solomon Basin imply this species has had a long history in the region (Dorsey 2000).

Two nonindigenous bivalves have established large populations in Kansas and continue to extend their ranges within the state (Figs. A45 and A46). The Asian clam (Veneroida: Corbiculidae: *Corbicula fluminea* [Müller, 1774]) was discovered initially during the early 1980s (Mackie and Huggins 1983; Cope 1985) and currently is found in all but one major river basin (Upper Republican). In some favorable habitats, this animal attains population densities of 250–500 individuals (adults and juveniles) m⁻² (e.g., Angelo et al. 2007). The zebra mussel (Veneroida: Dreissenidae: *Dreissena polymorpha* [Pallas, 1771]) was discovered originally in August 2003 in the Walnut Basin (El Dorado Lake). This bivalve has expanded its range in the Walnut Basin and also now occurs in the Kansas/Lower Republican Basin (Perry Lake), the Lower Arkansas Basin (Cheney Reservoir, Lake Afton), and the Neosho Basin (Marion Lake). Maximum reported population densities in Kansas have approached 30,000 individuals m⁻² (El Dorado Lake; J.M. Goeckler, pers. comm. 2008). In comparison, densities as high as several hundred thousand individuals m⁻² have been documented

in some other states and provinces (e.g., Claudi and Mackie 1994).

DISCUSSION

Freshwater mussel distributions in Kansas are controlled by a broad combination of natural and anthropogenic factors. Key natural factors include the availability of perennially flowing streams, the composition and stability of the benthic substrate, and stream drainage patterns influencing the dispersal of host fishes. Mussel diversity gradually decreases from east to west across the state (Appendix 1), coinciding with a marked reduction in annual average precipitation (Goodin et al. 1995), a decline in the permanency of stream flow (Perry et al. 2004), a higher incidence of sand and shifting sand substrata west of the 97th meridian (Cross 1967), and a decrease in the number of host species (Cross 1967; Cross and Collins 1995). In eastern Kansas, mussel diversity in many streams increases progressively from the spring-fed, nutrient-poor headwater segments to the warmer and more productive downstream segments (e.g., Angelo et al. 2007). Mussels in western Kansas are confined (or historically were confined) primarily to smaller tributaries containing relatively stable substrata (Hoke 1997).

Natural lakes are rare in Kansas, whereas artificial impoundments (ponds and reservoirs) and lakes occupying abandoned quarries and other excavations (pit lakes) now number in the hundreds of thousands (KDHE 2005a). A few mussel species attain high population densities in many smaller impoundments and pit lakes (Table 1). Unconfirmed reports from commercial shell collectors also point to significant populations of *A. plicata*, *P. purpuratus*, *Q. metanevra*, and *Q. quadrula* in the upper reaches of a few large reservoirs (Mosher 2007). Some of these reports are unprecedented geographically and may signify the occurrence of new populations originating from the release of bait fish or hatchery-reared fish infested with glochidia (see Gangloff and Gustafson 2000). Unfortunately, artificial lakes fail to accommodate the habitat demands of most native mussel species. Dissolved oxygen requirements, silt tolerances, reproductive strategies, fish host preferences, and other factors generally restrict the distribution of these bivalves to perennially flowing streams (Murray and Leonard 1962).

Droughts lasting for several years are a recurring phenomenon in Kansas (Weaver and Alberton 1936; Bryson 1980) and have led to the temporary cessation of stream flow in large areas of the state (Mead 1896; Deacon 1961; Clement 1991; Putnam et al. 2008). These events

undoubtedly have diminished or eliminated many local mussel populations (see Metcalf 1983). Formerly, the resumption of stream flow and the return of host fishes from spring-fed tributaries, permanent pools, and distant stream reaches facilitated the gradual recovery of these populations. Today, dams (large and small), floodgates, culverts, and other impediments to fish migration hinder or preclude the reestablishment of mussels in many watersheds (see Watters 1996; Vaughn and Taylor 1999; Dean et al. 2002).

Dams create additional problems for freshwater mussels. Most notably, the ponds and reservoirs formed by these structures are unusually susceptible to the invasion of nonindigenous fish, shellfish, and other aquatic organisms, including certain forms clearly inimical to native mussels and their host species (Fig. A46) (see Gido et al. 2002; Mammoliti 2002; Eberle 2007b; KDHE 2008). Flood-control reservoirs commonly retain storm-water runoff during late spring and early summer, thereby diminishing the seasonal peak flows associated with spawning in many riverine host fishes (see Cross and Moss 1987; Eberle 2007b). In years of excessive precipitation, some large reservoirs discharge vast quantities of accumulated water well into the late summer or early fall, seasons normally characterized by low stream flow and important for mussel reproduction (Murray and Leonard 1962). These prolonged discharges often destabilize the downstream benthic substrate, displacing juvenile mussels, hampering interactions between gravid mussels and host fishes, and in severe cases eliminating entire mussel assemblages (see Vaughn and Taylor 1999).

Agriculture is another powerful force shaping mussel distributions in Kansas (Angelo et al. 2004). The onset of row-crop production during the middle and late 1800s resulted in widespread soil erosion, and many of the state's most productive mussel beds and fish-spawning areas were blanketed in silt during this period (Mead 1896; Metcalf 1966; see also Doze 1924; Franzen and Leonard 1943). Although much emphasis was placed subsequently on the mitigation of this problem (Devlin 2000), stream siltation remains a pervasive concern and a limiting factor for mussels in numerous water bodies (Obermeyer et al. 1995; Hoke 1996, 2005; KDHE 2008). Livestock customarily have had access to riparian areas and stream channels throughout much of Kansas, and the seasonal confinement of small herds to sheltered locations near streams remains a common practice in this state (e.g., many cow-calf and winter feeding operations). In some locations, livestock have exacerbated the effects of siltation by overgrazing riparian vegetation, trampling stream banks, and compacting the benthic substrate supporting

mussels (e.g., Hoke 1997). Problems related to substrate compaction are most severe during extended droughts, when surface flows decline (or cease altogether) and livestock congregate for long periods near the remaining pools in the stream channels (Angelo 1994).

Nearly all surface waters in Kansas have been contaminated measurably with chemicals used in agriculture (KDHE 2008). The runoff of nitrogen- and phosphorus-containing fertilizers has led to recurring algal blooms, compositional changes in benthic and suspended microbial communities, and cascading effects on filter-feeding organisms and the broader aquatic food web (see Smith et al. 1999; Nichols and Garling 2000; Downing et al. 2001; Patzner and Müller 2001; Egertson and Downing 2004). Herbicides such as atrazine and metolachlor are detected routinely in surface water and sporadically in fluvial sediment (Carney et al. 1991; Pope 1995, 1998; KDHE 2008). Some insecticides no longer in use (e.g., dieldrin, DDT, various degradation products) persist in sediment and the fatty tissues of fish and shellfish (Havlik and Marking 1987; Pope 1998; Juracek 2004). The combined effects of these compounds on mussels and other aquatic organisms are poorly understood, but the potential for endocrine system disruption and other physiological complications has received growing scientific scrutiny (Cheney et al. 1997; Xie et al. 2005; Suzawa and Ingraham 2008).

Other agricultural contaminants have exerted a more obvious and immediate impact on the regional mussel fauna. For instance, prior to the enactment of state and federal laws regulating the disposal of livestock wastes, pollution from feedlots and slaughterhouses (primarily in the form of unionized ammonia and oxidizable solids) devastated the fish and invertebrate communities of many surface waters in eastern Kansas (Cross and Braasch 1968; Gray 1968; Prophet 1969; Cross and Cavin 1971; Prophet and Edwards 1973). The Cottonwood River (Neosho Basin) received large quantities of feedlot runoff and ranked as one of the state's most heavily contaminated water bodies during the 1960s (e.g., Prophet 1969). Although water quality conditions have improved in recent decades (A.J. Stahl, pers. comm. 2008), some segments of the Cottonwood River now support only half their original number of mussel species (Table 2).

Irrigated crop production in western Kansas has exacted a heavy toll on mussels and other aquatic life by lowering groundwater tables, reducing or eliminating spring flows, transforming perennial streams into intermittent or ephemeral systems, and diminishing the available dilution base for contaminants entering surface waters (Jordan 1982; Cross et al. 1985; Cross and Moss

1987; Angelo 1994; Hoke 1997; Schloss et al. 2000; Eberle et al. 2002; Eberle 2007b). Throughout much of Kansas, but especially in the northeastern portion of the state, many streams have been channelized to expedite storm-water runoff, decrease local flooding, and improve access to farm fields. This practice has destroyed or severely degraded numerous aquatic habitats and dramatically reduced fish and shellfish diversity (Hoke 1996; see also Witt 1970). Intensive crop production also has led to the draining and filling of many marshes, sloughs, oxbows, and other wetlands in Kansas. By the late 20th century, the state had lost about half its presettlement wetland surface area (Dahl 1990). This change undoubtedly reduced the overall abundance of certain rapidly growing and short-lived mussel species capable of exploiting wetland habitats (e.g., *A. suborbiculata*) (see Schuster 1978; Schuster and DuBois 1979).

Several other anthropogenic factors have played (or soon will play) an important role in the decline of the regional mussel fauna. First, urban and residential sprawl, sand and gravel dredging operations, mining activities (coal, salt, lead, zinc), oil field development, and discharges from storm sewers, factories, and wastewater treatment plants all have altered the physical and chemical properties of many surface waters in Kansas. These factors typically have affected individual water bodies (or individual watersheds) rather than broad regions of the state, but their collective impacts on mussels and other aquatic organisms have been substantial (Doze 1926; Jones 1950; Branson 1963; Cross et al. 1982; Angelo et al. 2002, 2007; KDHE 2008; see also Fuller 1974; Goudreau et al. 1993; NNMCC 1998). Second, mussels have been harvested commercially in the state for more than a century. Demand for mussel shells was fueled originally by the mother-of-pearl industry (Coker 1919) and later by the Asian cultured pearl industry (Cope 1983; Mosher 2007). Harvest pressures have led to precipitous declines in some local mussel populations but have had little apparent impact on mussel distributions (Murray and Leonard 1962; Miller and Mosher 2008). Third, certain fishes serving as biological hosts for larval mussels have been extirpated from entire river basins or the state as a whole (see Haslouer et al. 2005). These losses probably have accelerated the range reductions occurring in several mussel species, including some rapidly declining T/E species (e.g., *Q. cylindrica cylindrica*, Fig. A31) (Mulhern et al. 2002). Fourth, and perhaps most importantly, the invasion and spread of the zebra mussel poses an unprecedented threat to indigenous mussel populations (Fig. A46). Zebra mussels attach themselves in large numbers to the shells

of other bivalves, competing for food and interfering with normal respiration, movement, and valve closure. These animals already have decimated native mussel communities in some areas of eastern North America (e.g., Strayer and Smith 1996; Ricciardi et al. 1998).

Despite these pressing conservation concerns, freshwater mussels have demonstrated at times an impressive capacity for population recovery. Miller and Lynott (2006) documented rapidly increasing densities of several mussel species in a biological sanctuary established in the middle Verdigris River (Verdigris Basin). They attributed these increases to the cessation of commercial mussel harvests within the sanctuary, to the renovation of an upstream sewage treatment plant, and to the aggressive implementation of soil conservation practices within the watershed, leading to lower levels of suspended solids in the river. Angelo et al. (2007) recently documented 10 mussel species in the lower Spring River (Neosho Basin), a stream reach once bereft of mussels owing to pollution from lead and zinc mining operations. The return of these animals coincided with gradual improvements in water and sediment quality following closure of the mines. Proposed revisions to the national surface water quality criteria for certain heavy metals, residual chlorine, and unionized ammonia are expected to benefit mussels and other aquatic organisms, provided these revisions are adopted by federal, state, and tribal water quality agencies (Augspurger et al. 2003; Wang et al. 2007). Furthermore, regulations controlling the commercial harvest of native mussels have become increasingly restrictive in recent decades (Busby and Horak 1993). In 2003, Kansas enacted a moratorium on all such harvests to encourage the recovery of heavily exploited mussel species (Mosher 2007). Kansas also has implemented a program for limiting the spread of zebra mussels and other invasive aquatic species, but the logistical, budgetary, and regulatory challenges confronting this program are admittedly daunting (Goeckler 2005).

A few exceptional streams in Kansas continue to support all, or nearly all, of their historical assortment of freshwater mussel species (Table 2). Several other streams and a few oxbows and marshes retain viable populations of at least one rare mussel taxon. Assuming these surface waters are protected from further degradation, they should provide much of the seed material needed by governmental agencies and other organizations implementing mussel propagation and restocking programs (*see* Obermeyer 2000, 2002; Barnhart 2002). Some mussel populations in Kansas display unique morphological and developmental attributes (e.g., Eckert

2003) or are distinguishable genetically from counterpart populations in the eastern United States (Barnhart 2001; Serb 2006; Burdick and White 2007). Cooperative efforts between natural resource agencies, landowners, and the general public are needed to avert the extirpation of these distinctive populations. The survey findings discussed and illustrated in this report provide a well-documented baseline for future mussel conservation and recovery efforts in Kansas.

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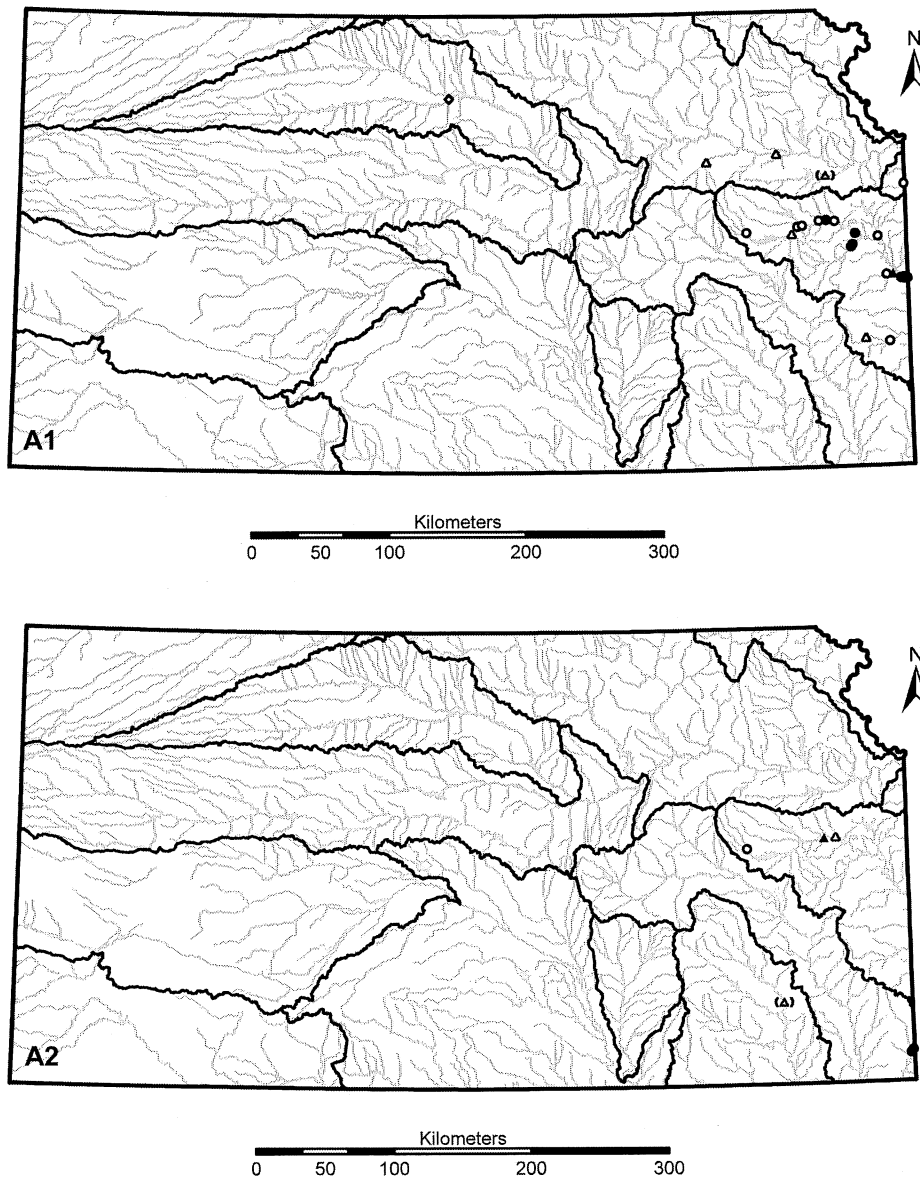
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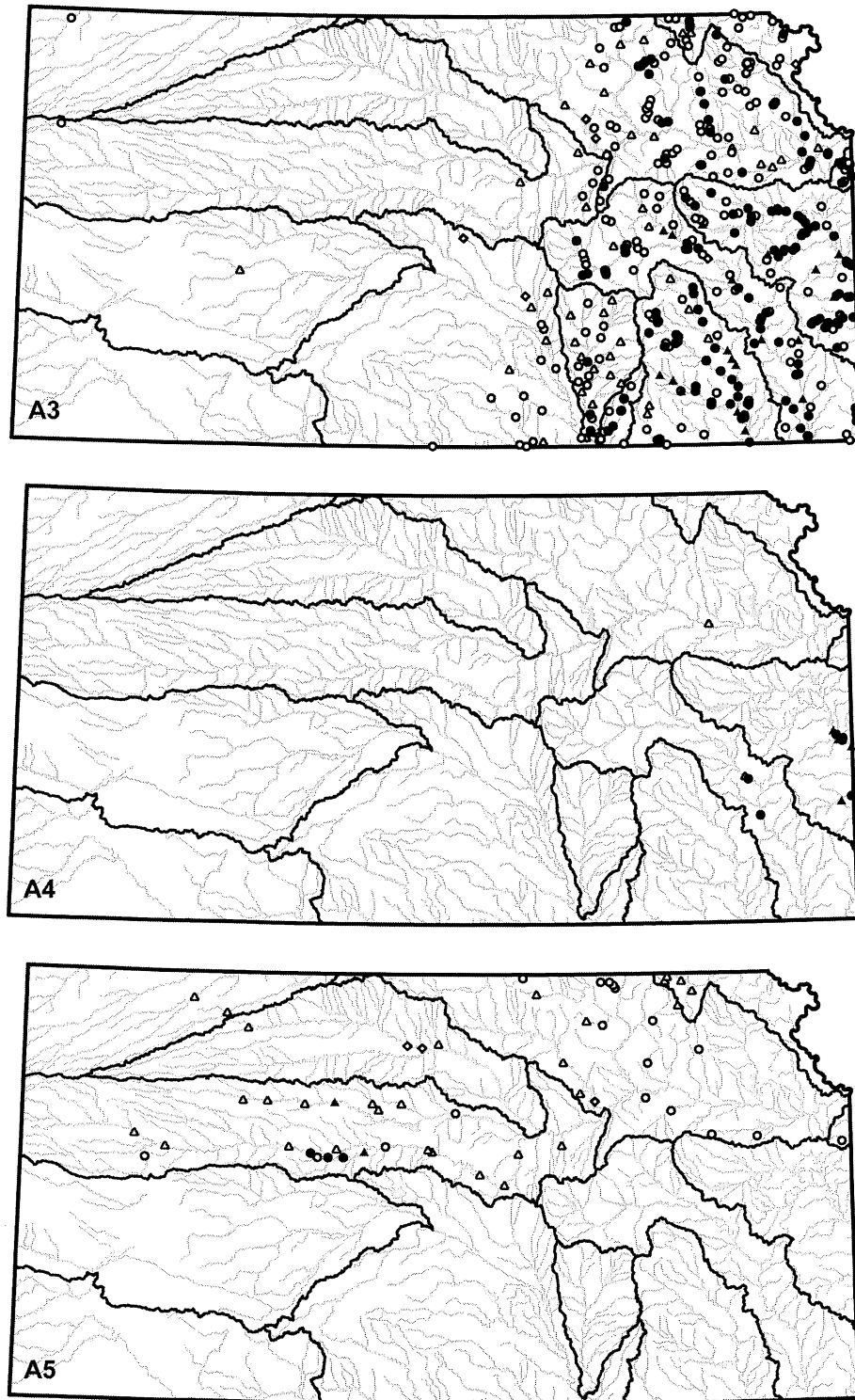
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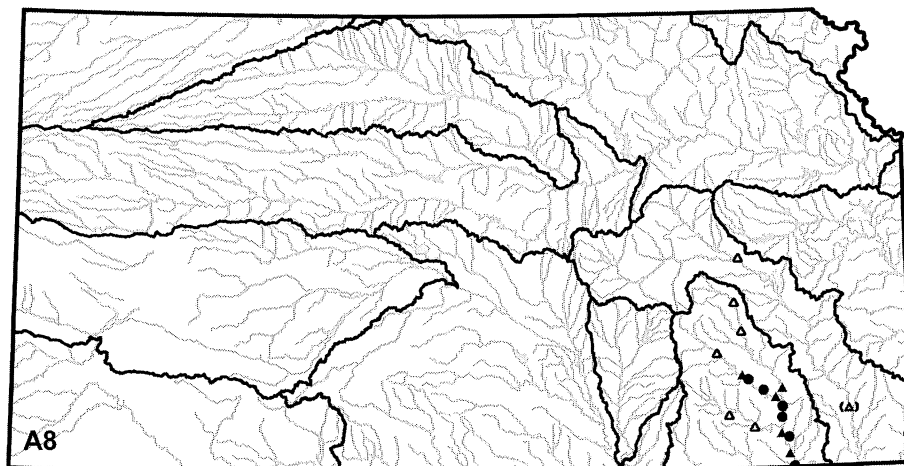
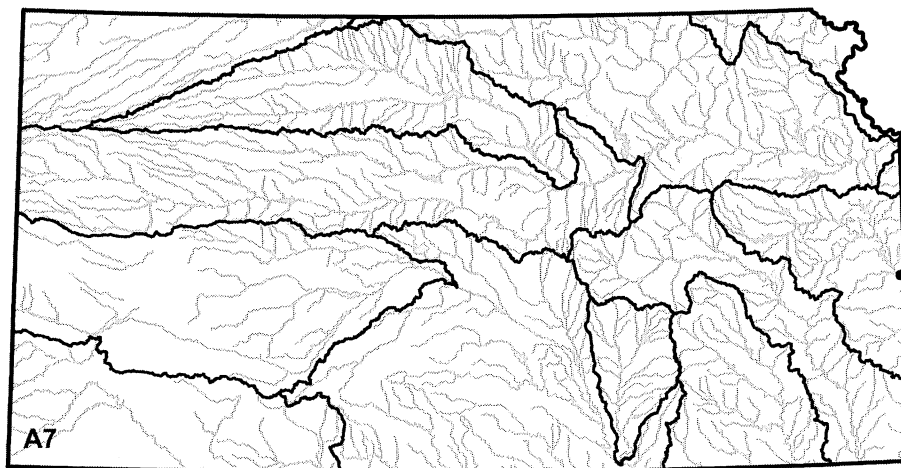
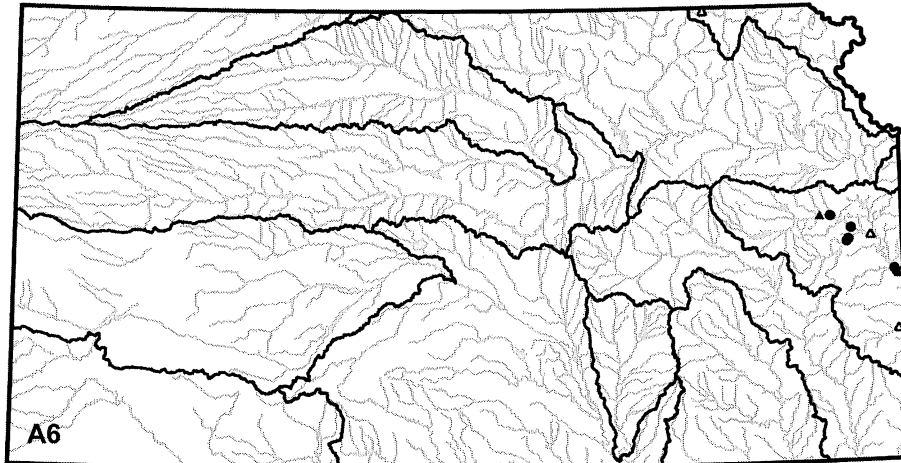
APPENDIX 1
FRESHWATER MUSSEL DISTRIBUTIONS IN KANSAS



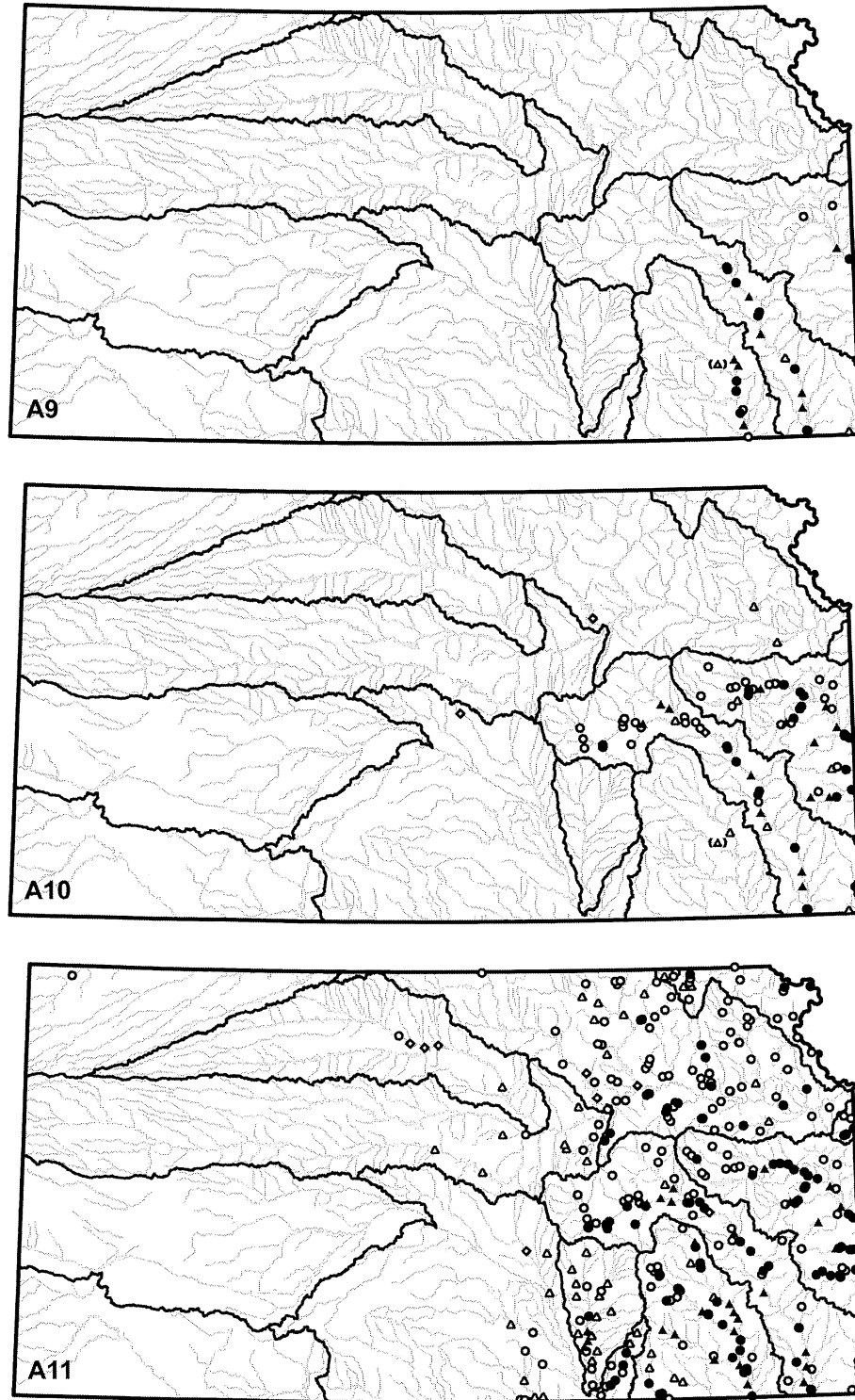
Figures A1 and A2. Distributions of *Actinonaias ligamentina* (A1) and *Alasmidonta marginata* (A2). In these maps and the maps that follow, sites sampled for mussels during 1990–2007 and supporting the indicated species are shown as solid circles (KDHE/KDWP surveys) or solid triangles (other surveys). Sites yielding only weathered or subfossil shell materials, and other formerly productive sites lacking recent evidence of the species, are shown as open circles (KDHE/KDWP surveys), open triangles (other surveys; museum collections), open diamonds (archeological studies), or open squares (paleontological studies). Sites mentioned in historical documents but lacking specific locality data are depicted as open symbols within parentheses. Directional arrows and scale bars are omitted intentionally from the remaining maps. Informational sources other than KDHE and KDWP are identified in Appendix 2.



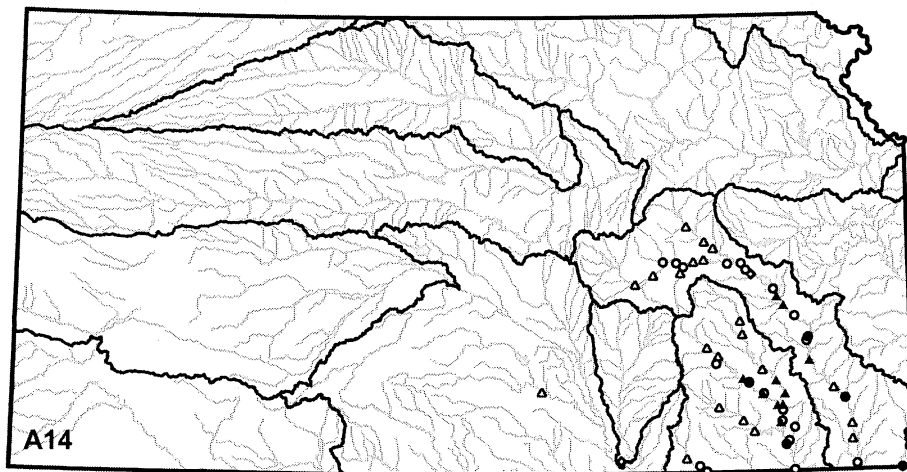
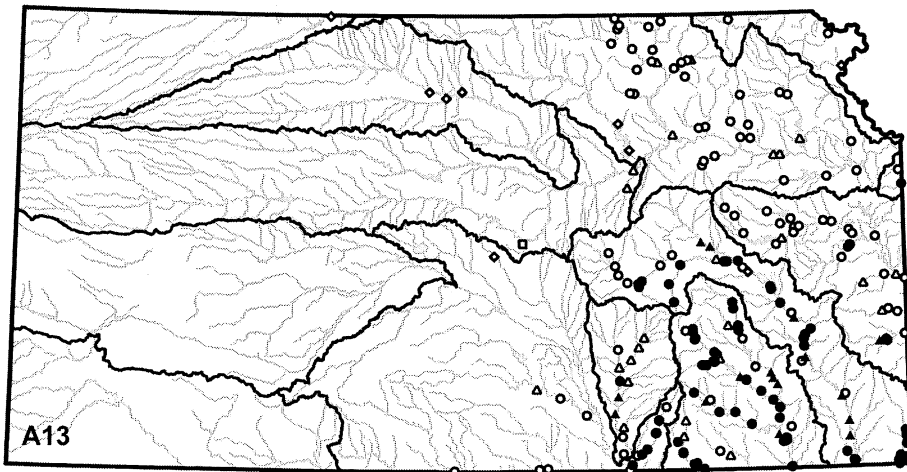
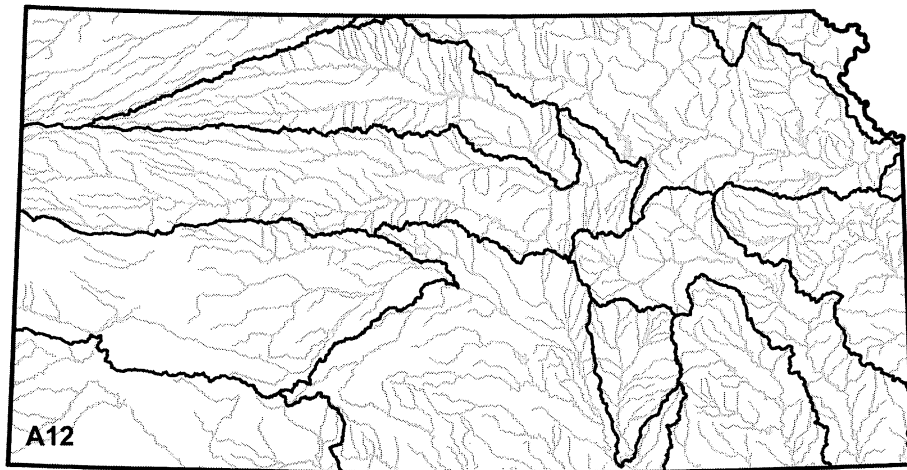
Figures A3–A5. Distributions of *Amblesma plicata* (A3), *Anodonta suborbiculata* (A4), and *Anodontoides ferussacianus* (A5).



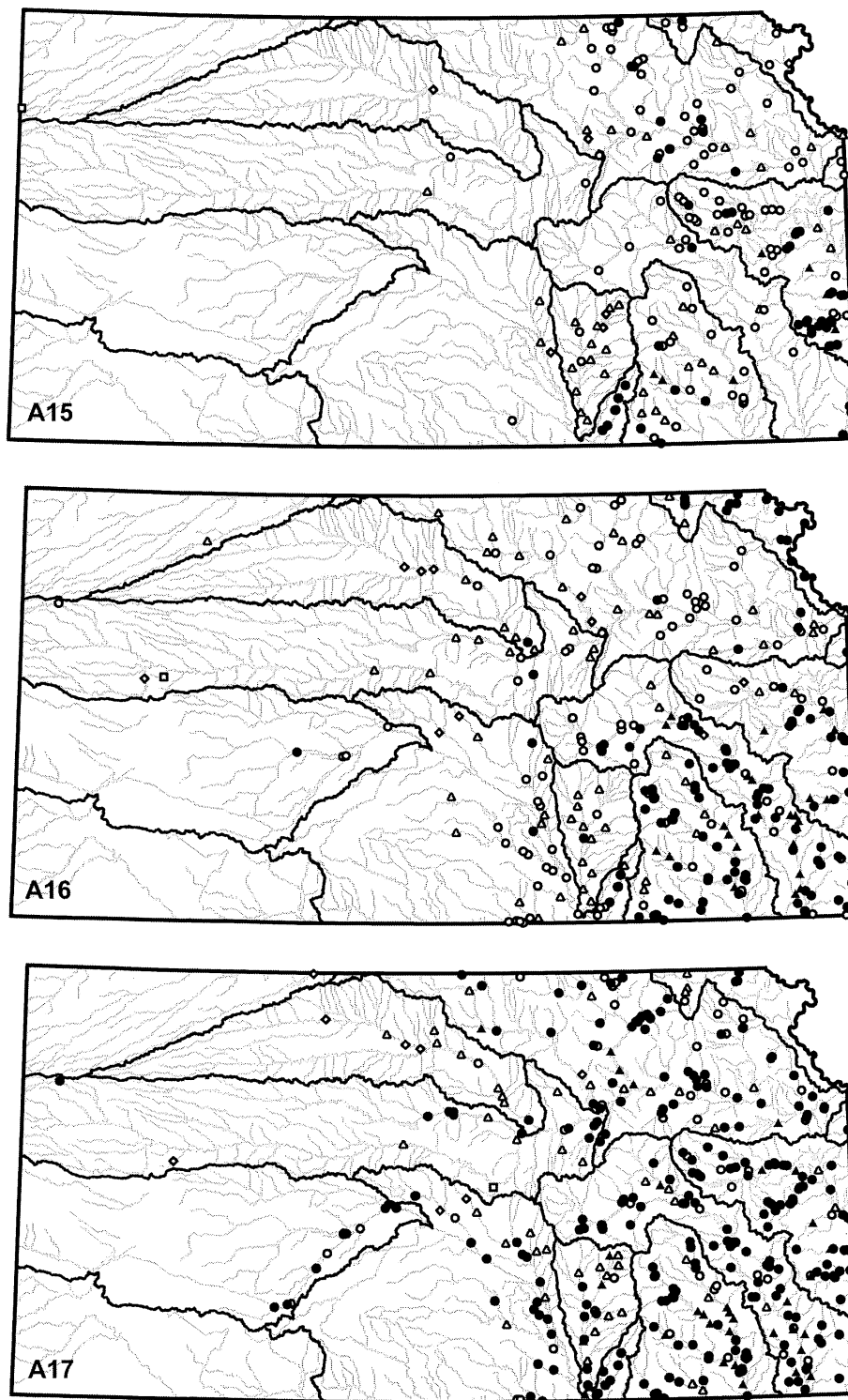
Figures A6–A8. Distributions of *Arcidens confragosus* (A6), *Cyclonaias tuberculata* (A7), and *Cyprogenia aberti* (A8).



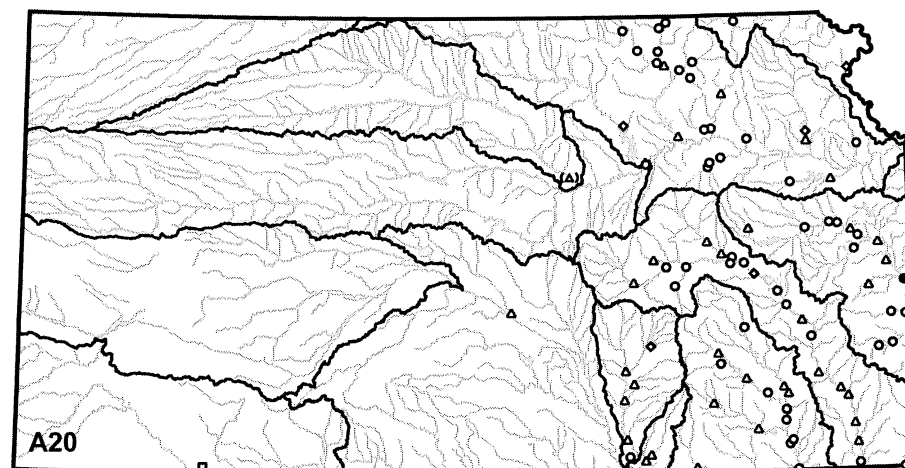
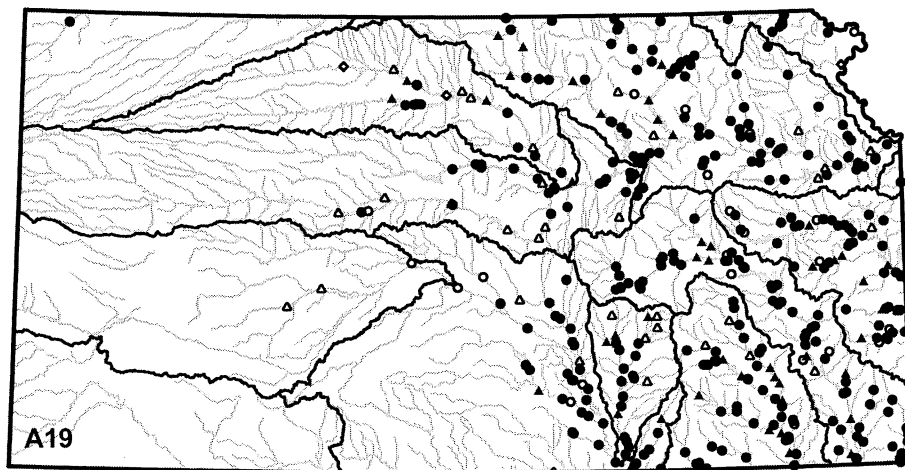
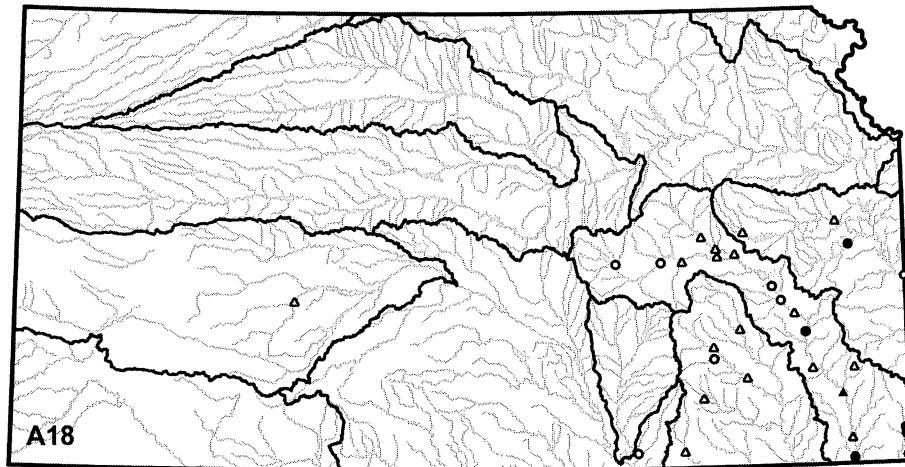
Figures A9–A11. Distributions of *Ellipsaria lineolata* (A9), *Elliptio dilatata* (A10), and *Fusconaia flava* (A11).



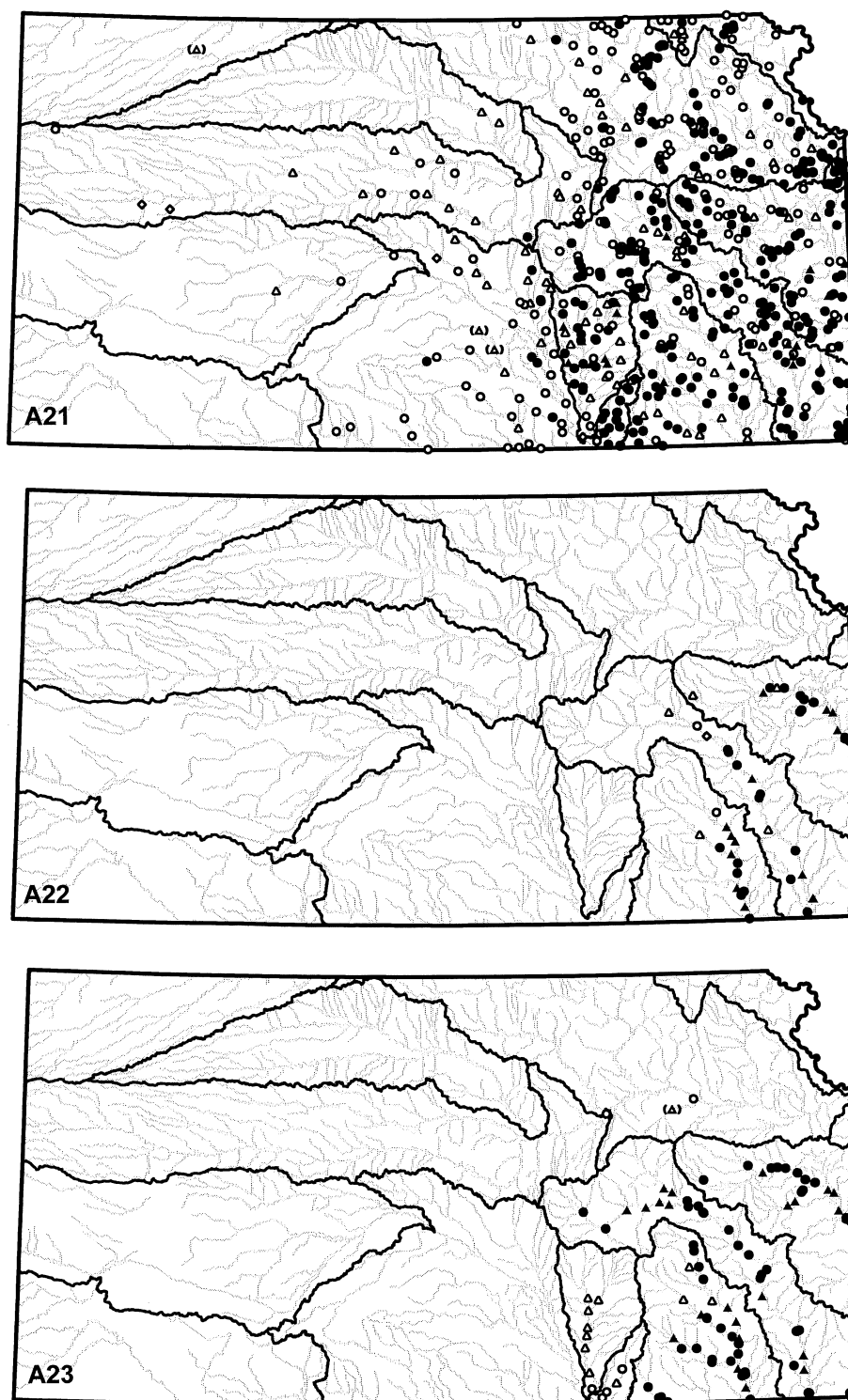
Figures A12–A14. Distributions of *Fusconaia ozarkensis* (A12), *Lampsilis cardium* (A13), and *Lampsilis rafinesqueana* (A14).



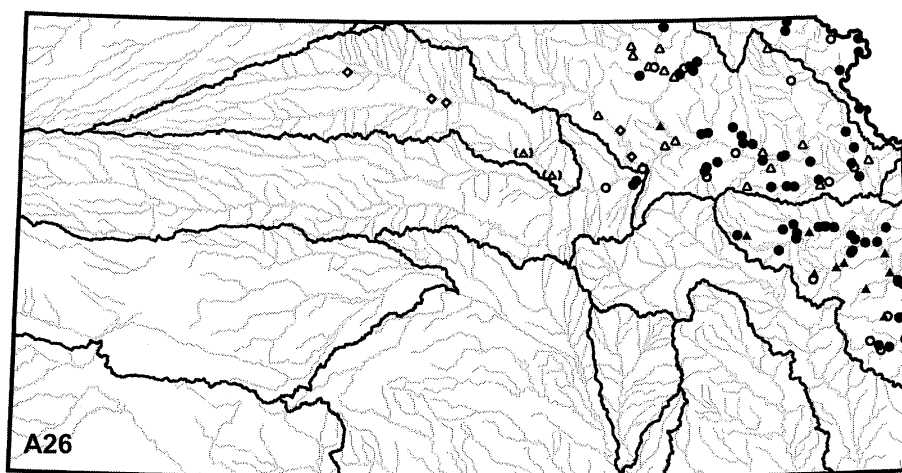
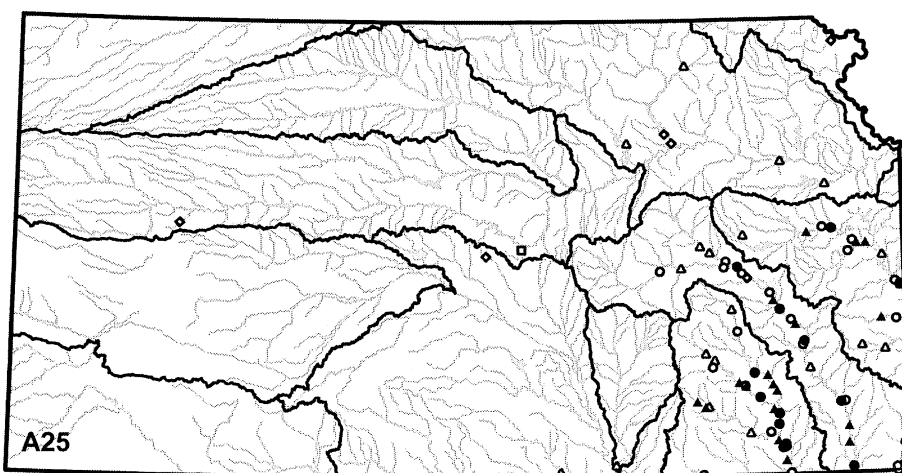
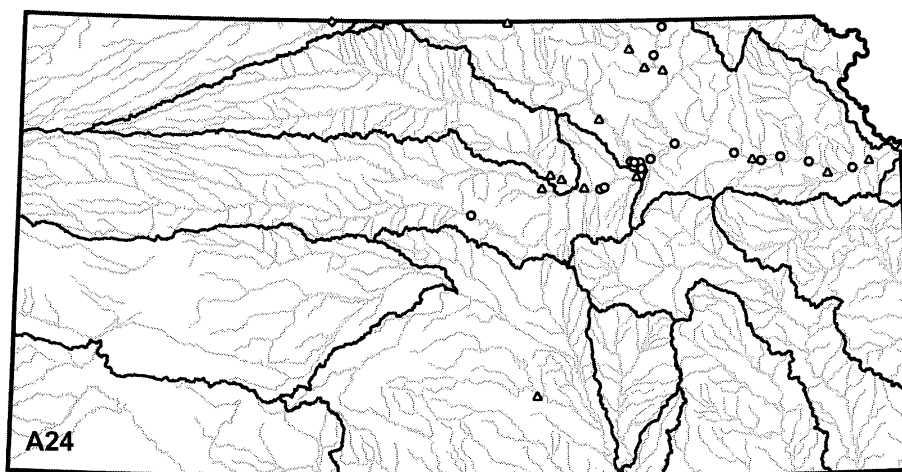
Figures A15–A17. Distributions of *Lampsilis siligoidea* (A15), *Lampsilis teres* (A16), and *Lasmgona complanata complanata* (A17).



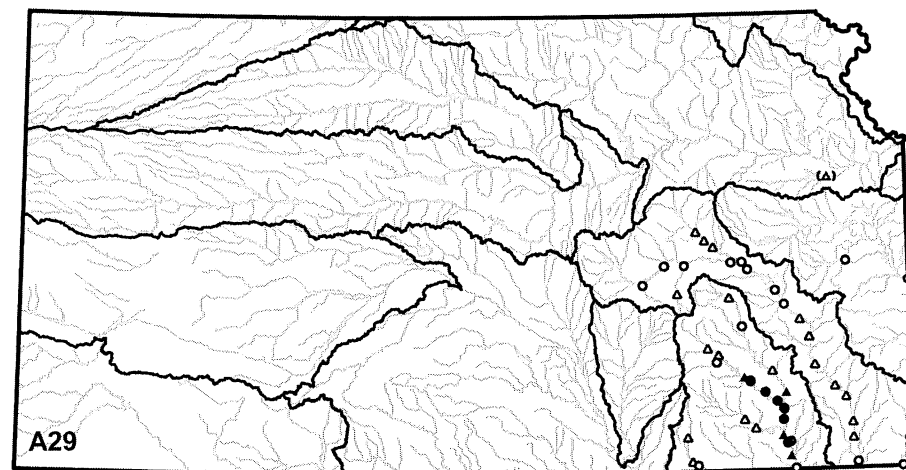
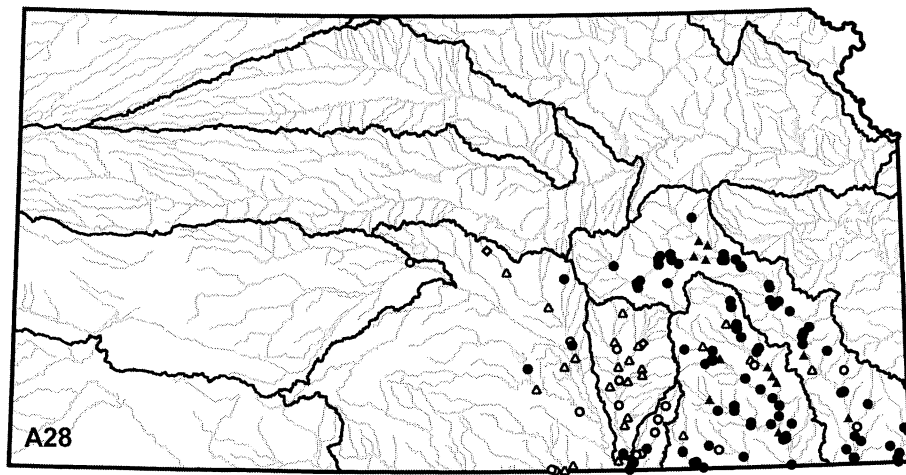
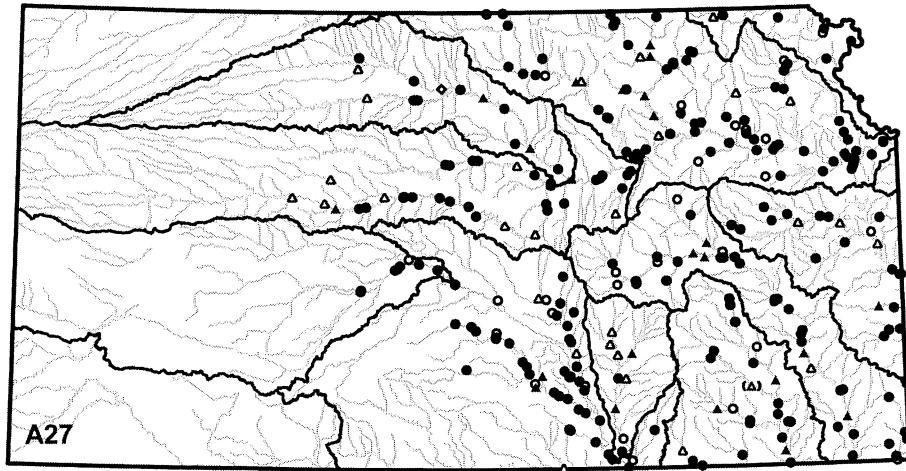
Figures A18–A20. Distributions of *Lasmigona costata* (A18), *Leptodea fragilis* (A19), and *Ligumia recta* (A20).



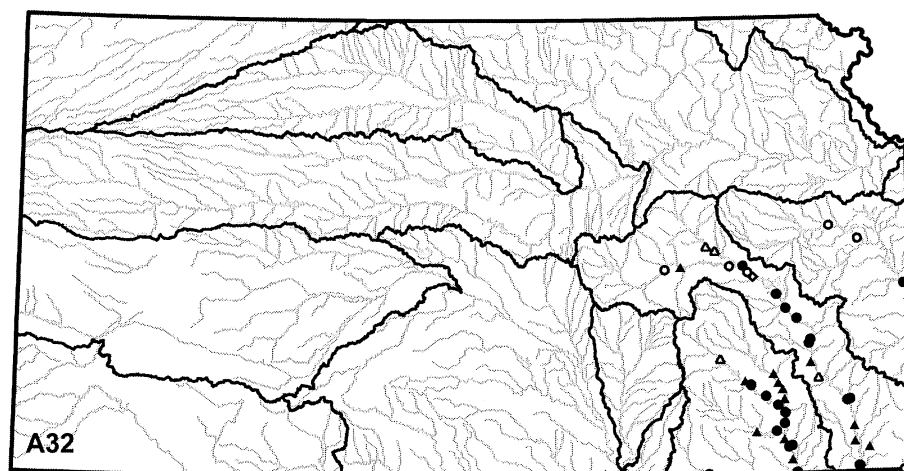
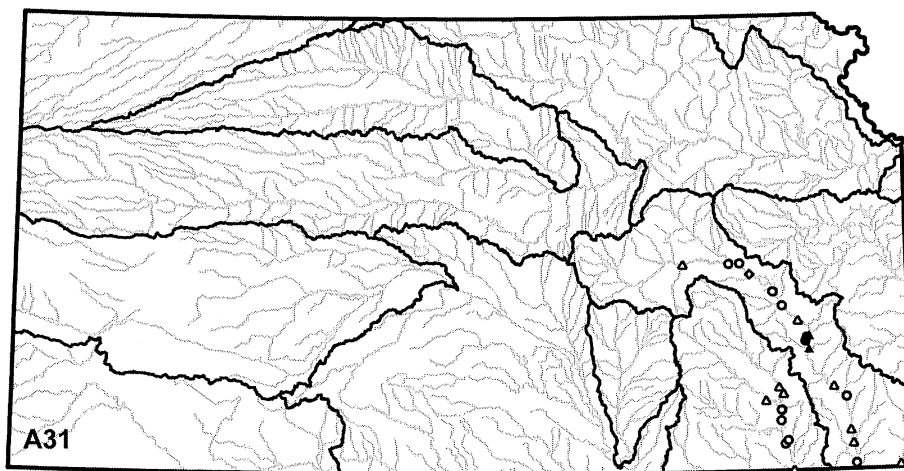
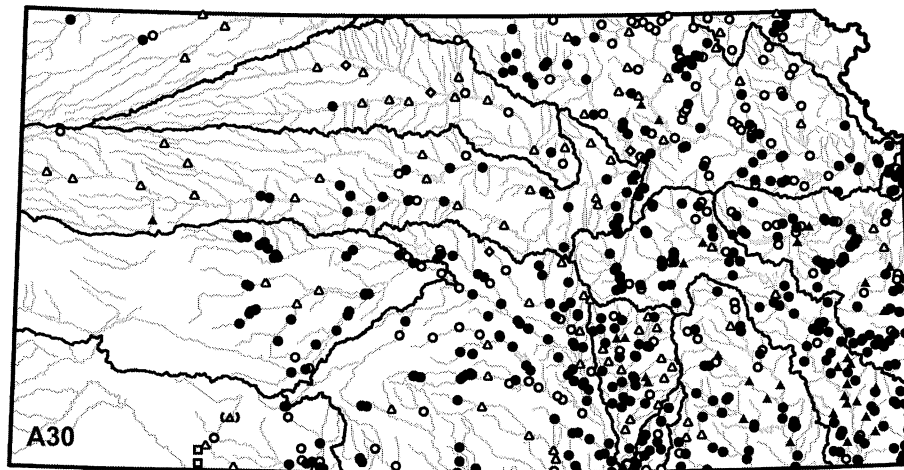
Figures A21–A23. Distributions of *Ligumia subrostrata* (A21), *Megaloniais nervosa* (A22), and *Obliquaria reflexa* (A23).



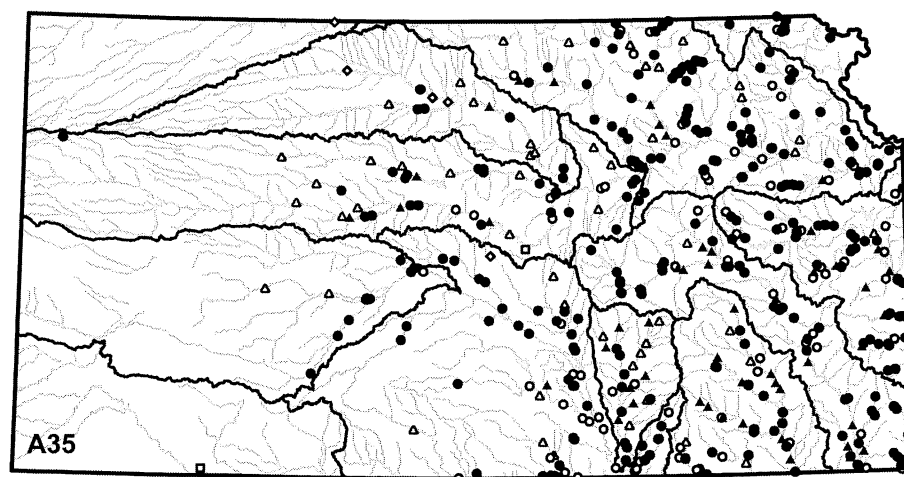
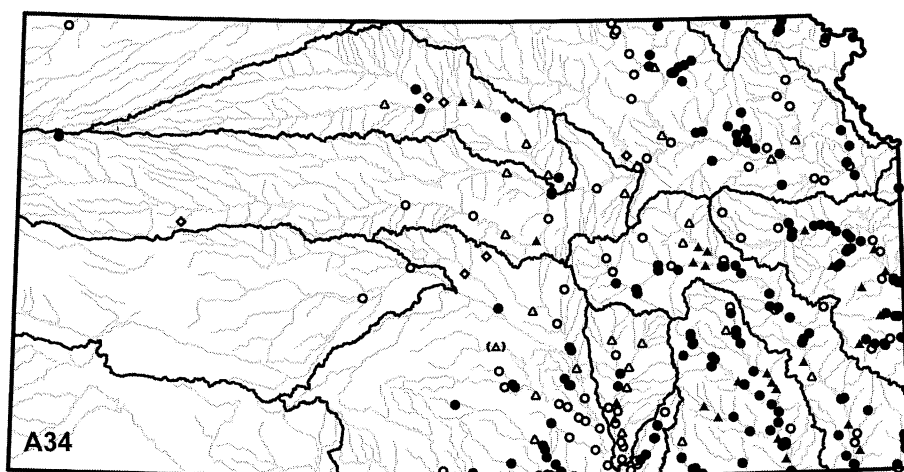
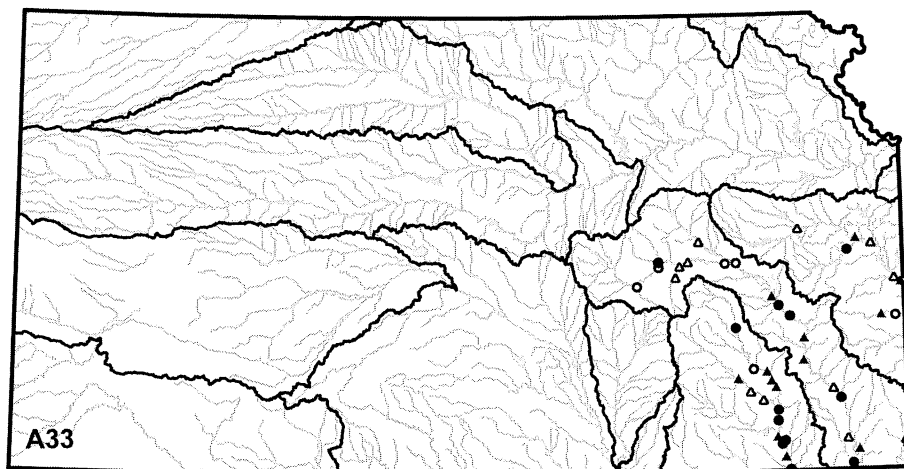
Figures A24–A26. Distributions of *Obovaria olivaria* (A24), *Pleurobema sintoxia* (A25), and *Potamilus alatus* (A26).



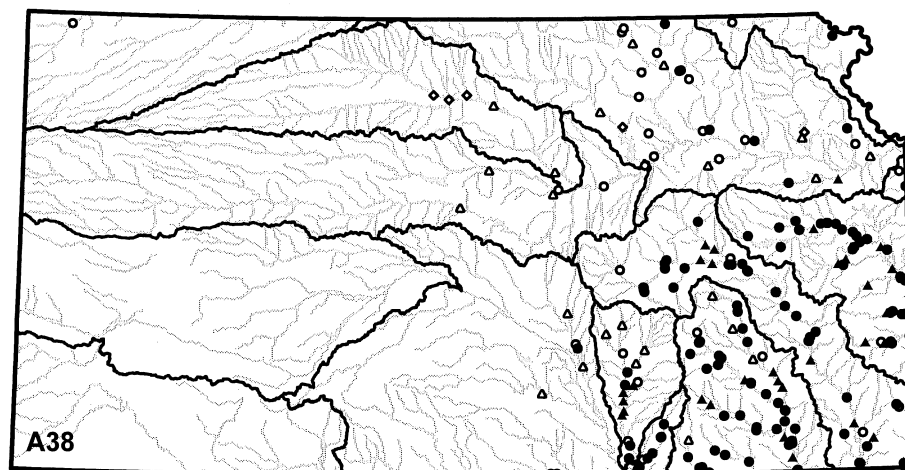
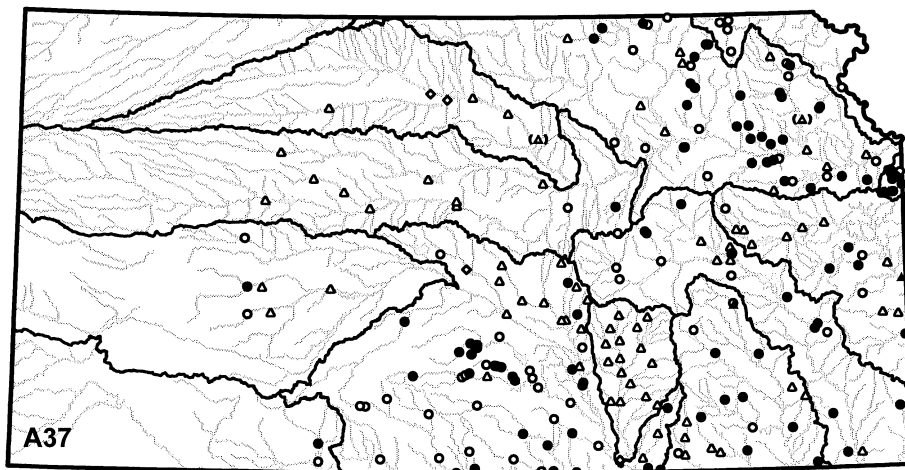
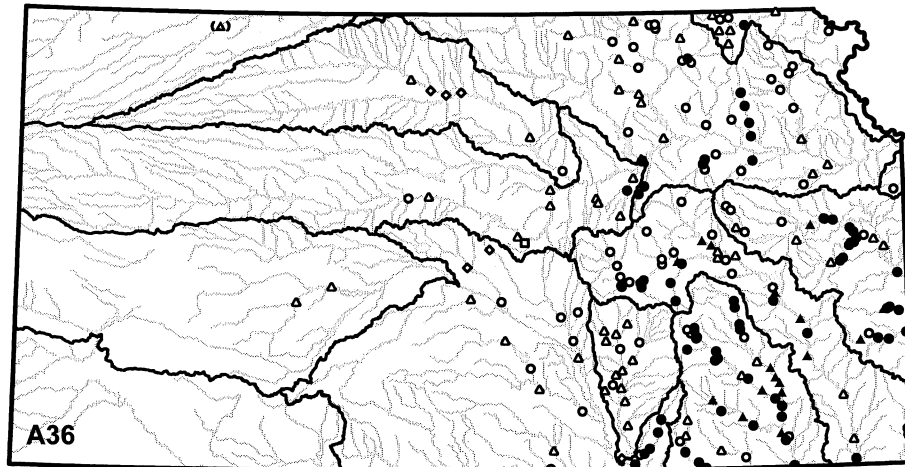
Figures A27–A29. Distributions of *Potamilus ohiensis* (A27), *Potamilus purpuratus* (A28), and *Ptychobranchus occidentalis* (A29).



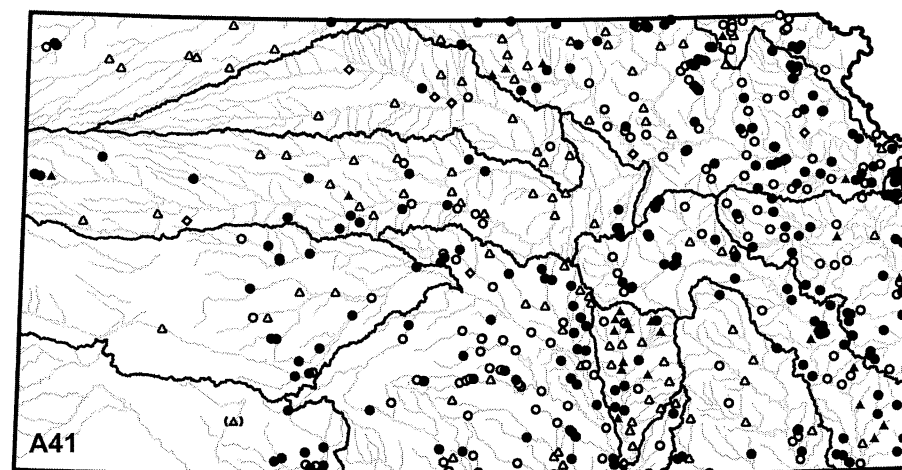
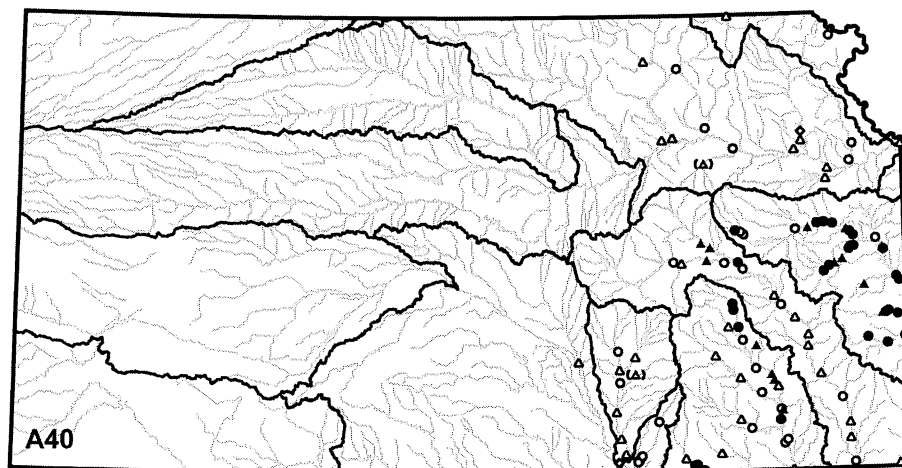
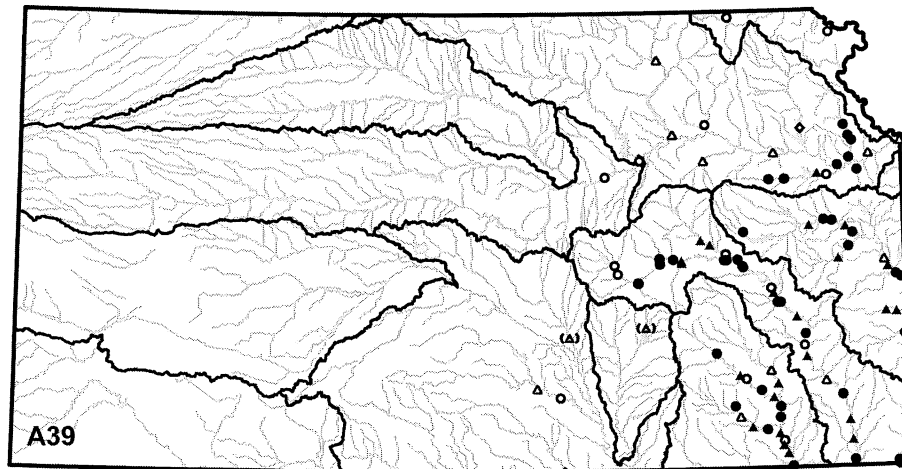
Figures A30–A32. Distributions of *Pyganodon grandis* (A30), *Quadrula cylindrica cylindrica* (A31), and *Quadrula metanevra* (A32).



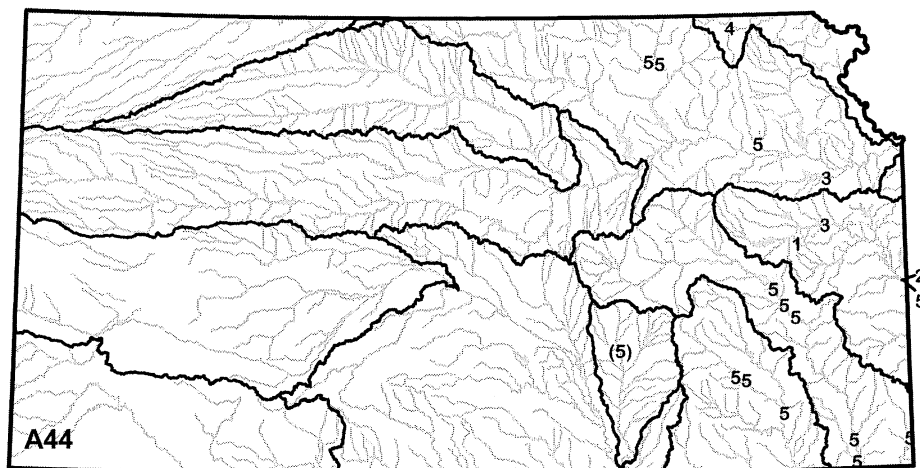
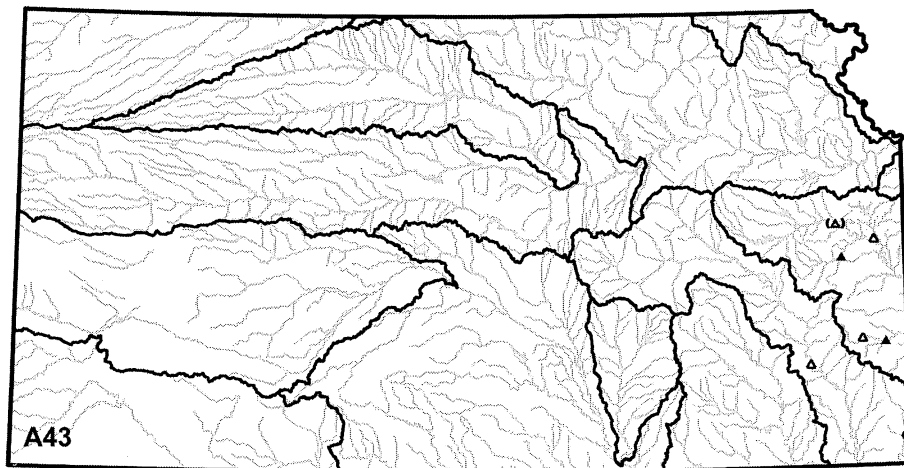
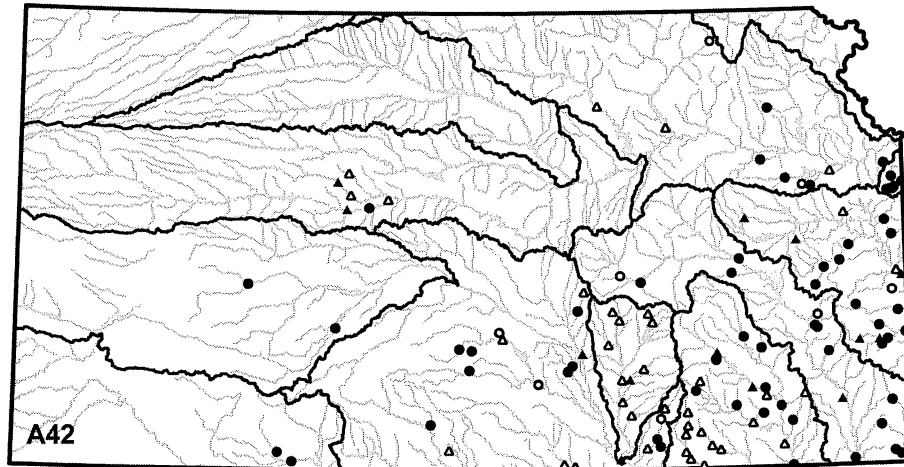
Figures A33–A35. Distributions of *Quadrula nodulata* (A33), *Quadrula pustulosa pustulosa* (A34), and *Quadrula quadrula* (A35).



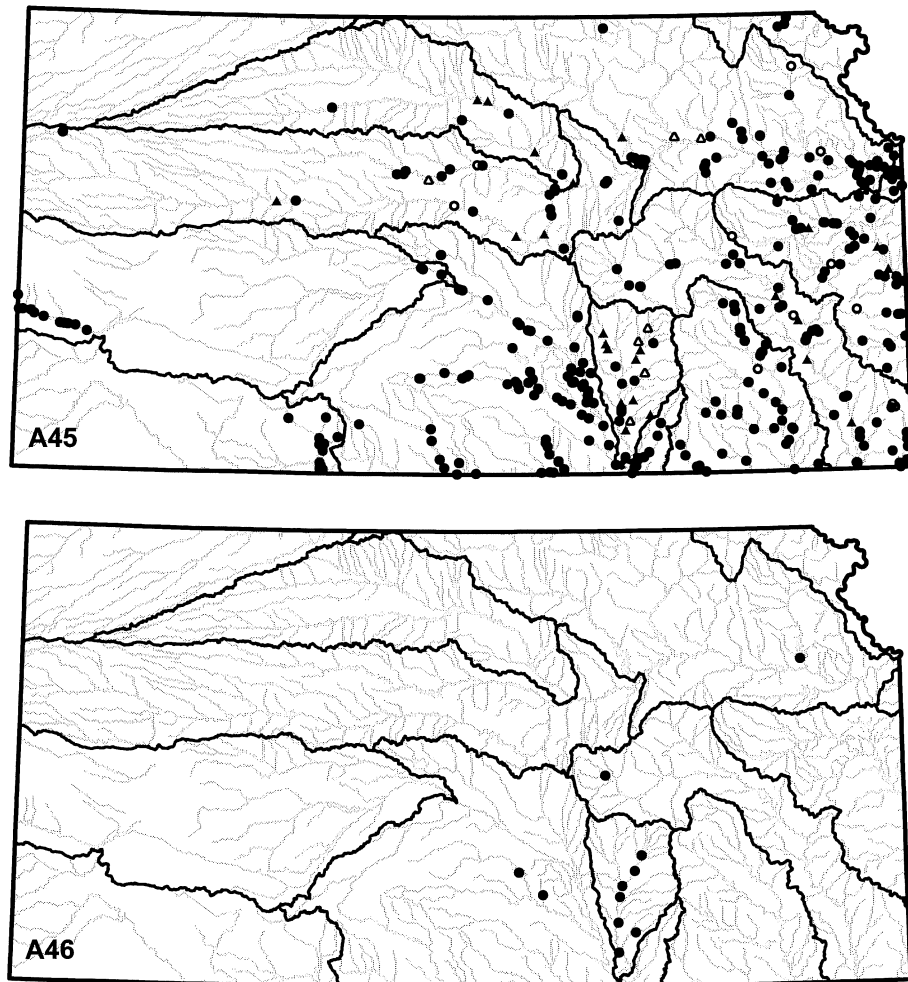
Figures A36–A38. Distributions of *Strophitus undulatus* (A36), *Toxolasma parvus* (A37), and *Tritogonia verrucosa* (A38).



Figures A39–A41. Distributions of *Truncilla donaciformis* (A39), *Truncilla truncata* (A40), and *Uniomerus tetralasmus* (A41).



Figures A42–A44. Distributions of *Utterbackia imbecillis* (A42) and *Venustaconcha ellipsiformis* (A43) and former distributions of five extirpated species represented in voucher collections (A44): *Alasmidonta viridis* (1), *Cumberlandia monodonta* (2), *Epioblasma triquetra* (3), *Lasmigona compressa* (4), and *Quadrula fragosa* (5).



Figures A45 and A46. Distributions of two nonindigenous bivalves: *Corbicula fluminea* (A45) and *Dreissena polymorpha* (A46).

APPENDIX 2
SOURCES OF SUPPLEMENTAL DATA USED IN MUSSEL DISTRIBUTIONAL MAPS

Figure	Data sources
A1	Call (1885a); Scammon (1906); Grinnell (1942); Liechti and Huggins (1977); Dorsey (1998); D.J. George, pers. comm. (2008)
A2	NMNH 86193; Distler and Bleam (1987); K.J. Couch, pers. comm. (2008)
A3	Call (1885a, 1885c, 1886); Popenoe (1885); Scammon (1906); Grinnell (1942); Franzen and Leonard (1943); Leonard and Leonard (1946); Wedel (1959); Frazier (1977); Schuster (1979); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Thies (1981); Hunter (1993); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Vanleeuwen and Arruda (2001); Combes (2003); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A4	Call (1885c); Scammon (1906); Schuster and DuBois (1979); D.J. George, pers. comm. (2008)
A5	Call (1885b, 1887); Miller and Hibbard (1972); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Dorsey (1998); R.E. Warren, pers. comm. (2008)
A6	Cope (1979); Hoke (1996); Couch (1997); Obermeyer (2001a); T.J. Menard, pers. comm. (2008)
A7	(no supplemental data used in map)
A8	Call (1887); Murray and Leonard (1962); Obermeyer et al. (1995); Combes (2003); Wolf and Stark (2005); Mosher (2006)
A9	Call (1887); Cope (1979); Obermeyer et al. (1995); Wolf and Stark (2005); Mosher (2006)
A10	Call (1885c, 1887); Scammon (1906); Grinnell (1942); Wedel (1959); Thies (1981); Obermeyer et al. (1995); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A11	Baker (1909); Grinnell (1942); Franzen and Leonard (1943); Leonard and Leonard (1946); Wedel (1959); Miller and Hibbard (1972); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Thies (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); Combes (2003); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A12	(no supplemental data used in map)
A13	Call (1885a, 1885c); Scammon (1906); Grinnell (1942); Leonard and Leonard (1946); Kivett (1953); Wedel (1959); Miller (1970); Hacker (1980); Metcalf (1980); Thies (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1997, 2005); Dorsey (1998); Reed (2002); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A14	UMMZ 52426; Call (1886); Grinnell (1942); Branson (1966); Cope (1979); Thies (1981); Distler and Bleam (1995); Obermeyer et al. (1995, 1997); Wolf and Stark (2005); D.E. Bleam, pers. comm. (2008)
A15	Call (1885b, 1886, 1887); Popenoe (1885); Grinnell (1942); Franzen and Leonard (1943); Leonard and Leonard (1946); Wedel (1959); Murray and Leonard (1962); Miller and Hibbard (1972); Liechti and Huggins (1977); Hacker (1980); Metcalf (1980); Cope (1981); Obermeyer et al. (1995); Bleam and Distler (1996); Couch (1997); Obermeyer (2001b); Reed (2002); Hoke (2004); Mosher (2006); Warren and Holen (2007); R.E. Warren, pers. comm. (2008)
A16	Call (1885b, 1886, 1887); Popenoe (1885); Scammon (1906); Grinnell (1942); Franzen and Leonard (1943); Wedel (1959); Murray and Leonard (1962); Wilmeth (1970); Miller and Hibbard (1972); Frazier (1977); Schuster (1979); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Thies (1981); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Dean et al. (2002); Reed (2002); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A17	Call (1885b, 1887); Popenoe (1885); Mead (1896); Grinnell (1942); Franzen and Leonard (1943); Kivett (1953); Wedel (1959); Murray and Leonard (1962); Miller (1970); Frazier (1977); Hacker (1980); Cope (1981); Hunter (1993); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Couch (1997); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); Wolf and Stark (2005); Mosher (2006); Tiemann (2006); R.E. Warren, pers. comm. (2008)

APPENDIX 2 (continued)

Figure	Data sources
A18	Call (1886, 1887); Grinnell (1942); Cope (1979); Metcalf (1980); Obermeyer et al. (1995); Combes (2003)
A19	Call (1885b, 1886, 1887); Grinnell (1942); Wedel (1959); Murray and Leonard (1962); Miller and Hibbard (1972); Frazier (1977); Schuster (1979); Hacker (1980); Claassen (1981); Cope (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Couch (1997); Hoke (1997, 2005); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); Combes (2003); Wolf and Stark (2005); Mosher (2006); Tiemann (2006); R.E. Warren, pers. comm. (2008)
A20	USNM (NMNH) 134446; Call (1885c); Scammon (1906); Grinnell (1942); Wedel (1959); Murray and Leonard (1962); Miller (1966); Frazier (1977); Cope (1979); Hacker (1980); Metcalf (1980); Thies (1981); Witty (1983); Obermeyer et al. (1995); Reed (2002); Sherraden et al. (2002); Combes (2003); Hoke (2005); Wolf and Stark (2005); R.E. Warren, pers. comm. (2008)
A21	Call (1885c, 1886, 1887); Popenoe (1885); Grinnell (1942); Leonard and Leonard (1946); Wedel (1959); Murray and Leonard (1962); Miller and Hibbard (1972); Frazier (1977); Schuster (1979); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Vanleeuwen and Arruda (2001); Reed (2002); U.S. Fish and Wildlife Service (2003); Mosher (2006); Tiemann (2006); D.E. Bleam, pers. comm. (2008)
A22	Call (1887); Grinnell (1942); Murray and Leonard (1962); Thies (1981); Obermeyer et al. (1995); Vanleeuwen and Arruda (2001); Wolf and Stark (2005); Mosher (2006)
A23	Call (1885c); Leonard and Leonard (1946); Obermeyer et al. (1995); Hacker (1980); Reed (2002); Combes (2003); Wolf and Stark (2005); Mosher (2006)
A24	UMMZ 107481; Call (1886); Scammon (1906); Kivett (1953); Distler and Bleam (1995); Hoke (1997, 2004, 2005)
A25	Call (1885a, 1885b, 1886, 1887); Scammon (1906); Baker (1909); Grinnell (1942); Wedel (1959); Murray and Leonard (1962); Branson (1966); Miller (1970); Liechti and Huggins (1977); Thies (1981); Obermeyer et al. (1995); Combes (2003); Hoke (2005); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)
A26	Call (1885b, 1886); Popenoe (1885); Scammon (1906); Grinnell (1942); Franzen and Leonard (1943); Liechti and Huggins (1977); Obermeyer et al. (1995); Bergman (1998); Dorsey (1998); Combes (2003); Hoke (2004, 2005); Wolf and Stark (2005); Tiemann (2006); Mosher (2006); R.E. Warren, pers. comm. (2008)
A27	Popenoe (1885); Scammon (1906); Murray and Leonard (1962); Miller and Hibbard (1972); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Dorsey (1998); Reed (2002); Mosher (2006)
A28	Call (1885c, 1886); Leonard and Leonard (1946); Wedel (1959); Murray and Leonard (1962); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Hunter (1993); Distler and Bleam (1995); Obermeyer et al. (1995); Reed (2002); Combes (2003); Mosher (2006)
A29	UMMZ 154036; Call (1885b, 1886); Frazier (1977); Cope (1979); Metcalf (1980); Obermeyer et al. (1995); Mosher (2006)
A30	Call (1885c, 1887); Popenoe (1885); Grinnell (1942); Leonard (1943); Leonard and Leonard (1946); Wedel (1959); Hibbard and Taylor (1960); Murray and Leonard (1962); Miller and Hibbard (1972); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Hunter (1993); Obermeyer et al. (1995); Bleam and Distler (1996); Hoke (1996, 1997, 2004, 2005); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); Sherraden et al. (2002); Wolf and Stark (2005); R.E. Warren, pers. comm. (2008)
A31	Call (1885c); Cope (1979); Thies (1981); Obermeyer et al. (1995); Mulhern et al. (2002)
A32	Thies (1981); Obermeyer et al. (1995); Vanleeuwen and Arruda (2001); Mosher (2006)
A33	Branson (1966); Cope (1979, 1983, 1985); Obermeyer et al. (1995); Vanleeuwen and Arruda (2001); Mosher (2006)
A34	Call (1885a, 1887); Grinnell (1942); Leonard and Leonard (1946); Wedel (1959); Miller and Hibbard (1972); Frazier (1977); Hacker (1980); Claassen (1981); Cope (1981); Distler and Bleam (1995); Hoke (1997, 2005); Dorsey (1998); Metcalf (1980); Obermeyer et al. (1995); Bergman (1998); Vanleeuwen and Arruda (2001); Reed (2002); Wolf and Stark (2005); Mosher (2006); R.E. Warren, pers. comm. (2008)

APPENDIX 2 (continued)

Figure	Data sources
A35	Call (1885b, 1885c); Grinnell (1942); Leonard and Leonard (1946); Kivett (1953); Wedel (1959); Hibbard and Taylor (1960); Miller (1970); Miller and Hibbard (1972); Frazier (1977); Schuster (1979); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1997, 2004, 2005); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); Wolf and Stark (2005); Mosher (2006); Tiemann (2006); R.E. Warren, pers. comm. (2008)
A36	Call (1885c, 1886, 1887); Popenoe (1885); Grinnell (1942); Franzen and Leonard (1943); Wedel (1959); Murray and Leonard (1962); Miller (1970); Liechti and Huggins (1977); Angelo (1978); Hacker (1980); Metcalf (1980); Cope (1981); Distler and Bleam (1995); Obermeyer et al. (1995); Bleam and Distler (1996); Hoke (1996, 1997, 2004, 2005); Dorsey (1998); Reed (2002); Wolf and Stark (2005); Mosher (2006); D.E. Bleam, pers. comm. (2008); R.E. Warren, pers. comm. (2008)
A37	Call (1885c, 1887); Popenoe (1885); Grinnell (1942); Wedel (1959); Murray and Leonard (1962); Miller and Hibbard (1972); Frazier (1977); Hacker (1980); Metcalf (1980); Cope (1981); Obermeyer et al. (1995); Hoke (1997, 2004, 2005); Bergman (1998); Dorsey (1998); Reed (2002); Combes (2003); U.S. Fish and Wildlife Service (2003); D.E. Bleam, pers. comm. (2008); R.E. Warren, pers. comm. (2008)
A38	UMMZ 73321; Call (1887); Scammon (1906); Grinnell (1942); Franzen and Leonard (1943); Leonard and Leonard (1946); Miller and Hibbard (1972); Schuster (1979); Hacker (1980); Metcalf (1980); Cope (1981); Witty (1983); Distler and Bleam (1995); Obermeyer et al. (1995); Hoke (1997, 2004, 2005); Bergman (1998); Dorsey (1998); Langley (2000); Vanleeuwen and Arruda (2001); Reed (2002); Wolf and Stark (2005); Mosher (2006); Tiemann (2006); R.E. Warren, pers. comm. (2008)
A39	Call (1885a, 1886, 1887); Popenoe (1885); Baker (1909); Murray and Leonard (1962); Liechti and Huggins (1977); Hacker (1980); Witty (1983); Distler and Bleam (1995); Obermeyer et al. (1995); Couch (1997); Combes (2003); Hoke (2005); Wolf and Stark (2005); Mosher (2006); Tiemann (2006)
A40	Call (1885a, 1885c, 1886, 1887); Popenoe (1885); Scammon (1906); Grinnell (1942); Leonard and Leonard (1946); Wedel (1959); Murray and Leonard (1962); Hacker (1980); Witty (1983); Obermeyer et al. (1995); Hoke (1996, 2004); Reed (2002); Wolf and Stark (2005); Mosher (2006); D.E. Bleam, pers. comm. (2008)
A41	Call (1885a); Grinnell (1942); Leonard (1943); Leonard and Leonard (1946); Wedel (1959); Murray and Leonard (1962); Miller and Hibbard (1972); Frazier (1977); Schuster (1979); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981); Witty (1983); Obermeyer et al. (1995); Hoke (1996, 1997, 2004, 2005); Couch (1997); Bergman (1998); Dorsey (1998); Vanleeuwen and Arruda (2001); Reed (2002); U.S. Fish and Wildlife Service (2003); Wolf and Stark (2005); Tiemann (2006); D.E. Bleam, pers. comm. (2008); R.E. Warren, pers. comm. (2008)
A42	Call (1887); Murray and Leonard (1962); Liechti and Huggins (1977); Hacker (1980); Metcalf (1980); Claassen (1981); Cope (1981, 1983); Hunter (1993); Bleam and Distler (1996); Hoke (1997, 2005); Bergman (1998); Obermeyer et al. (1995); Obermeyer (2001b); Sherraden et al. (2002); Combes (2003); U.S. Fish and Wildlife Service (2003); Mosher (2006); D.E. Bleam, pers. comm. (2008); M.K. Butler, pers. comm. (2008)
A43	FLMNH 269897; Call (1886); Scammon (1906); DuBois (1981); Mosher (2006)
A44 (1)	Bleam and Distler (1996)
A44 (2)	Mulhern et al. (2002)
A44 (3)	Scammon (1906)
A44 (4)	Hoke (1996)
A44 (5)	UMMZ 75811; Call (1885b, 1885c, 1886, 1887); Popenoe (1885); Isely (1925); Cope (1985); Bleam et al. (1998); Hoke (2004, 2005); K.J. Couch, pers. comm. (2008); B.R. Freske, pers. comm. (2008)
A45	Hunter (1993); Obermeyer et al. (1995); Hoke (1997, 2005); Bergman (1998); Reed (2002); Wolf and Stark (2005)
A46	(no supplemental data used in map)